

THE NERVOUS SYSTEM
AN ELEMENTARY HANDBOOK OF
ITS ANATOMY AND PHYSIOLOGY

BY
J. H. H. H. H. H. H.

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THE NERVOUS SYSTEM

THE NERVOUS SYSTEM

AN ELEMENTARY HANDBOOK OF THE ANATOMY
AND PHYSIOLOGY OF THE NERVOUS SYSTEM

FOR THE USE OF STUDENTS OF PSYCHOLOGY AND NEUROLOGY

BY

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PREFACE

THE steadily increasing application of physiological facts to problems in psychology, and the rapid development of the science of experimental psychology, have rendered it essential that the student of psychology should possess some knowledge of the anatomy and physiology of the nervous system of man. There are excellent articles on these in most of the recent textbooks of anatomy or of physiology, but generally the information is too detailed, and further, the student must of necessity purchase the complete book to acquire the desired article.

In this small textbook an attempt has been made to present the essential features of the anatomy and physiology of the nervous system in a form sufficiently simple to be understood by a non-medical student. At the same time it is hoped that it will prove useful, as an introductory handbook, for students of medicine, or for those who desire to refresh their memories of the central tracts, in considering cases of neurological interest.

The book makes no pretence of dealing with the application of the subject either to psychology or to neuro-pathology. It has been compiled from many sources but, obviously, it is impossible to acknowledge these individually. Most of the diagrams have been taken from 'Gray's Anatomy' (17th edition) and a few from 'Quain's Anatomy' (11th edition), by the courtesy of the editors and publishers of these works. The other diagrams are either original or are modifications of well-known figures.

The author desires to acknowledge with gratitude the great help he has received from Professor Howden, Professor of Anatomy in the University of Durham, under whose supervision the book has been written. He is also greatly indebted to Professor Robinson, Professor of Logic and Psychology in the University of Durham, who has kindly read over the MSS. and has generally defined the scope of the work.

UNIVERSITY OF DURHAM

COLLEGE OF MEDICINE,

Newcastle-on-Tyne, 1912.

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THE NERVOUS SYSTEM

CHAPTER I

THE ANIMAL CELL

THE essential constituent of all living matter is protoplasm, a translucent jelly-like material of complex structure. Its chemical composition cannot be determined by ordinary methods of analysis, since these inevitably entail the death of the protoplasm. The analysis yields a certain amount of information regarding the ultimate elements of which protoplasm is composed, but a knowledge of the manner of combination of these elements into definite compounds can only be obtained by observing the behaviour of protoplasm during life towards other chemical materials. When studied in this way, it soon becomes obvious that protoplasm cannot be regarded as a single definite chemical compound, but rather as a series of unstable, ever-varying groups, holding together under certain physiological conditions, but readily splitting asunder when these conditions alter.

In the animal body the protoplasm is divided up into small individual units known as cells. In the higher organisms these cells vary much in form and function, but all possess certain features in common. The main structural components of an animal cell are : (1) Protoplasm, (2) A nucleus ; but in addition there are present in the more complete cells, (3) A nucleolus, (4) Centrosomes and attraction spheres (Fig. 1).

Protoplasm.—Protoplasm is a viscid gelatinous material, containing a large proportion (about 75%) of water ; it may be either clear or granular. Under a high power of the microscope it is seen to consist of a slightly denser reticulum or network (spongioplasm), enclosed in the meshes of which is a more fluid portion (hyaloplasm).¹ Various other substances such as fat, pigment,

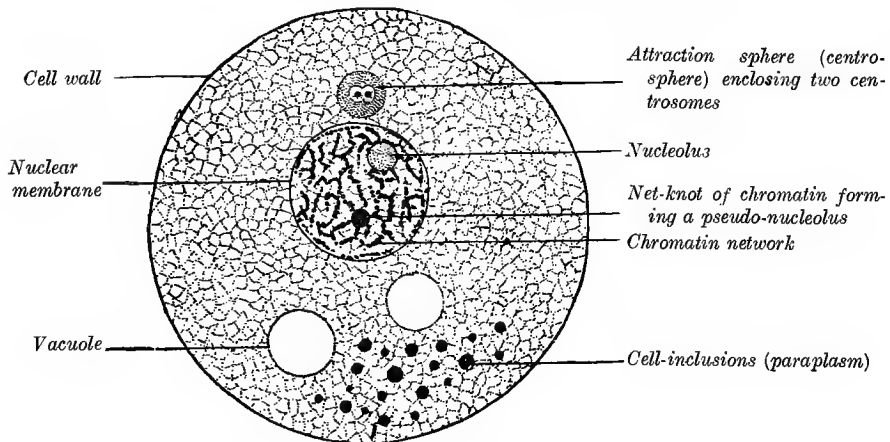
¹ This reticular structure of protoplasm is not absolutely constant. In many instances the structure might more properly be described as alveolar, while occasionally it may be granular or even homogeneous.

etc., may also be enclosed ; these are adventitious, and are termed cell inclusions or paraplasm.

Round the periphery of a cell is a fine membrane—the cell wall ; it is present in practically all cells, and is formed of materials generated by the activity of the protoplasm.

Nucleus.—A portion of the protoplasm within the cell is specially modified to form what is known as the nucleus. This body is usually of a spherical or oval form, and is separated from the general protoplasm (cytoplasm) by a delicate nuclear membrane. The nucleus, like the protoplasm from which it is derived, consists of hyaloplasm and an intranuclear network of spongioplasm. The nuclear spongioplasm presents, however, a most important difference from that of the cytoplasm ; it contains a number of bodies which stain very readily

FIG. 1.—Diagram of an animal cell. (Modified from Wilson.)



with certain dyes and are therefore called chromatin filaments. The nucleus is an exceedingly important component of the cell ; it cannot exist apart from the cytoplasm, while cytoplasm without a nucleus is inert and soon dies.

Nucleolus.—Within the nucleus one or more highly refracting particles are present ; they are termed nucleoli.

Centrosomes.—Immediately outside the nucleus are one, or frequently two, small bodies (centrosomes) forming the centres of spherical masses of densely-packed radiating protoplasmic granules. These spherical masses are known as attraction spheres ; they are seen best in cells which are undergoing division.

Properties of Protoplasm.—The chief characteristics of protoplasm are its powers of motion, nutrition, and reproduction. It possesses also the remarkable faculties of storing past impressions and of making provision for the future.

Within the cell, in many cases, a streaming movement of the protoplasm can be demonstrated; some surface cells, such as those of the respiratory passages, possess hair-like processes (cilia) which are constantly in motion so as to keep the surface free of deposited materials; but one of the most striking exhibitions of motile power is that presented by the white corpuscles of the blood. These corpuscles resemble greatly the unicellular organism, the *amœba*, and hence their movements are described as *amœboid*: a portion of the protoplasm is protruded from the cell as a finger-like process (pseudopodium) into which the rest of the mass is gradually drawn, and the whole cell thus shifts its position (Fig. 2). Associated with the protoplasmic movements other forms of energy are liberated which manifest themselves in electrical changes, chemical changes, heat, and occasionally light. The initiation of any or all of these changes is due to some alteration in the environment of the animal or cell; this alteration, which may be either chemical, mechanical, thermal, or photic, is known as the 'stimulus,' while the change in the cell is called the 'response.'

In order to maintain its energy, protoplasm has the power of selecting and taking up inert, nutritive substances and converting them into its own living material. As a necessary corollary to this it has also the power of extruding

FIG. 2.—Human white blood-corpuscle showing its successive changes of outline within ten minutes when kept moist on a warm stage. (Schofield.)

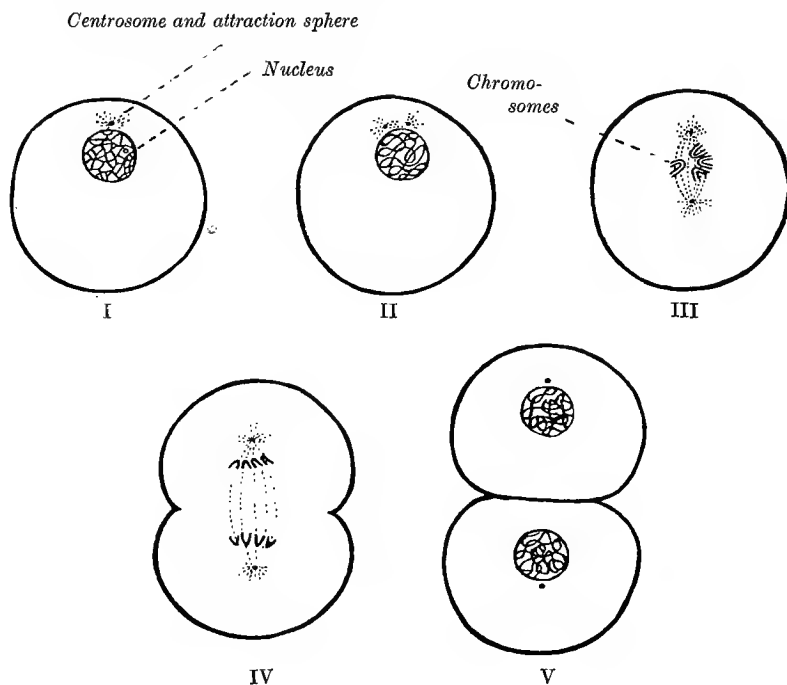


waste products resulting from the various chemical decompositions which accompany the manifestations of life. In multicellular organisms certain cells are specialised to act as manufactories for substances (secretions) required by the other cells, whilst other groups of cells take over and deal with the waste products of the organism (excretions).

All living cells are capable of reproducing themselves by subdivision. Only in a few instances is the subdivision effected by a simple cleavage or by budding off. In most cases a complex series of changes takes place, originating in the nucleus and centrosomes and later involving the cytoplasm; this process is known as indirect division, mitosis, or karyokinesis (Fig. 3). The nuclear membrane and the nucleolus disappear and the chromatin of the nucleus arranges itself in a spiral. The spiral soon breaks up into a fixed number of V-shaped portions which collect at the central zone or equator of the nucleus. Each V-shaped mass splits longitudinally into two and the resulting parts retreat to the two poles of the nucleus—an equal number to each—where they rearrange themselves again into spirals. A new nuclear membrane forms around the spiral and a new nucleolus appears. The cytoplasm becomes constricted opposite the equator of the original nucleus and by the deepening of this constriction the cell is ultimately split into two.

Genesis of Nerve Cells.—The nerve cells, while presenting many of the general characteristics described above, exhibit several modifications in details which will be considered in the next chapter. As, however, all cells have originated from cells similar to one another, it may be interesting to inquire into some of the factors which have determined the main peculiarities of the nervous tissues. It has already been pointed out that protoplasm is sensitive, i.e. has the power of responding to stimuli of various kinds. In the simplest forms of animal life the cells set apart to subserve the nervous func-

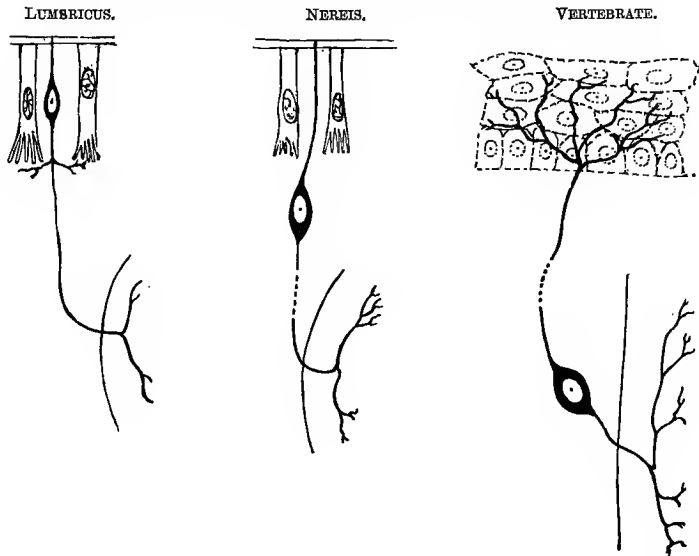
FIG. 3.—Diagram showing five stages in the process of cell-division by karyokinesis.



tions are essentially chosen for their high degree of sensitiveness to external stimuli, and their power of rapid response to such stimuli. As far as can be judged the varieties of stimulation to which they best respond are those of touch, temperature, and pain. Naturally they are cells on the surface of the organism, where they are in direct contact with changes in environment. In these simple animals they preside over the preservation of the animal's existence—ensuring a supply of nutrition and providing for efficient defence from noxious external forces. In animals higher in the scale of organisation, the differentiation of sex in individual animals introduces a new sphere of nervous activity.

The simple mechanism of a single cell receiving and responding to a stimulus is soon replaced by a double arrangement—one cell receives and transmits the impulse while the other responds. The receiving cell recedes from the surface for protection, leaving, however, a long filamentous portion of its protoplasm to collect and convey the stimuli (Fig. 4); another filament connects it with the responsive cell. As animals increase in size and complexity it becomes essential that

FIG. 4.—Diagrams showing the relative positions of the sensory cells in two worms (Lumbricus and Nereis) and in vertebrates. (After Retzius.)



The sensory nerve cells are shaded black; the ordinary surface cells are not shaded.

each receiving cell should be in communication with several responsive organs. The nervous system is therefore ultimately represented by two series of cells. The cells of one series have long processes stretching to the periphery for the reception and conveyance of impulses; the cells of the other series have processes reaching down to the responsive mechanisms—muscles, glands, etc. The two series are not in actual continuity but are in intimate contact with one another.

CHAPTER II

NERVE CELLS AND NERVE FIBRES

A. Histology

THE structural unit of the nervous system is a highly specialised cell consisting of a cell body (termed the nerve cell) and a series of processes; the

FIG. 5.—Neuron from spinal cord of man.
(Gerlach.)



complete unit is called a neuron (Fig. 5). The functional unit consists of a pair of such neurons (Fig. 6). One is destined for the reception of impulses from a sensory surface; it is generally described as the sensory neuron, since it is frequently associated with a sensation. The other discharges an impulse—as a rule to some motor mechanism, and is hence commonly known as the motor neuron.

The processes of every neuron, although similar in structure, are functionally of two kinds, and this is often emphasised by their grouping at two poles of the cell. One set of processes receives the stimulus from without and transmits the impulse to the cell; they are known as the dendrites or afferent (centripetal) processes. As a rule they emerge from the cell body as short thick stems which rapidly break up into series of fine branched filaments. The other group is usually represented by one long process which gives off side branches (collaterals) at intervals, and finally terminates in an arborisation like that of the dendrites. This process is known as the neurite, axon, or efferent (centrifugal) process.

It has already been indicated that each neuron has one long process directed towards the periphery of the body ; it will now be evident that in the case of the sensory neuron this process is a dendrite, while in the case of the motor neuron it is an axon.

Nerve Cells.—Nerve cells, being complete animal cells, consist of cytoplasm with nucleus, nucleolus, and centrosome. The cytoplasm is of special interest on account of : (a) its peculiar structure ; (b) certain differentiated masses in its interior.

(a) Running through the cytoplasm are many minute fibrils (neurofibrillæ) which are continuous with fibrils in the cell processes, indicating thus probable definite paths for the passage of impulses through the cell (Fig. 8).

(b) Embedded in the cytoplasm are small masses of granular material which stain deeply with aniline dyes. They are known as Nissl's granules or tigroid bodies, and consist of chromophilic material. They undergo alterations in

FIG. 6.—Scheme showing pair of neurons constituting a functional unit.

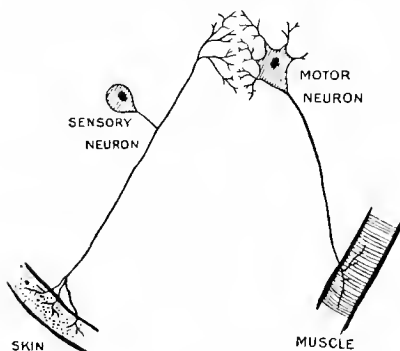
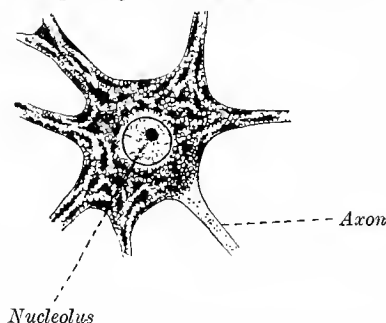


FIG. 7.—Motor nerve cell from ventral horn of spinal cord of rabbit. (After Nissl.) The angular and spindle-shaped tigroid bodies are well shown.



constitution and distribution during the activity of the cell. The cytoplasm also contains, in the vicinity of the nucleus, a certain amount of a yellowish-brown pigment (Fig. 7).

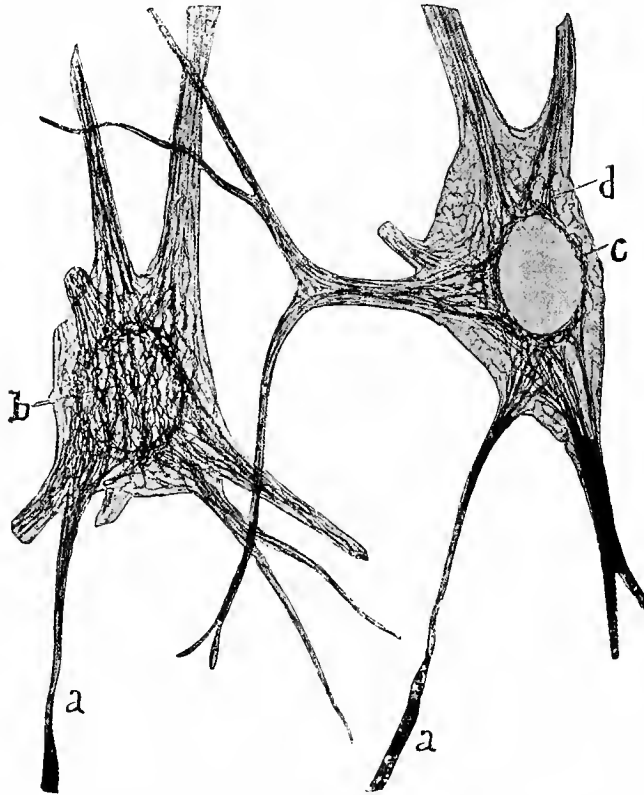
Nerve cells vary much in shape, and in many cases the form of the cell is characteristic of the region of the nervous system to which it belongs ; to a limited extent, therefore, it is also indicative of its function. According to their general shape, nerve cells may be divided into two classes : (A) Bipolar cells ; (B) Multipolar cells ; but the latter class is usually further divided into (a) cells of type I ; (b) cells of type II.

(A) *Bipolar Cells.*—Primarily each bipolar cell is a spindle-shaped cell with axon and dendrite emerging from opposite poles of the spindle (Fig. 9). In a few instances, e.g. the ganglia of the auditory nerve (nerve of hearing), this form is retained in the adult. Usually, however, the growth of the cell proceeds in a unilateral manner, with the result that the two poles gradually

fuse with one another to form a single process with a T-shaped or Y-shaped bifurcation. This is sometimes described as a unipolar cell (Fig. 10). The cells of the bipolar group belong to sensory neurons.

(B) *Multipolar Cells*.—Multipolar cells of type I. are occasionally spherical or pyramidal in shape, but are usually stellate or polygonal with groups of dendrites passing off from the various angles (Figs. 11 and 12). The point

FIG. 8.—Nerve cells of kitten, showing neurofibrillæ. (Cajal.)



a. Axon. b, c, d. Neurofibrillæ.

of origin of the axon is marked by a small elevation consisting of clear protoplasm free from pigment or tigroid bodies; this elevation is known as the implantation cone. These cells are the cell bodies of motor neurons, so that the axon is in all cases relatively long. The cells of type II. differ only in the relative length of the axon; in them the axon is short and soon breaks up into branches (Fig. 13).

Ganglia.—Most of the nerve cells are gathered together into a long central column forming the brain and spinal cord and known as the cerebro-spinal

axis. A few nerve cells, however, exist in groups apart from this—notably

FIG. 9.—Bipolar nerve cell from the spinal ganglion of the pike. (After Kölliker.)

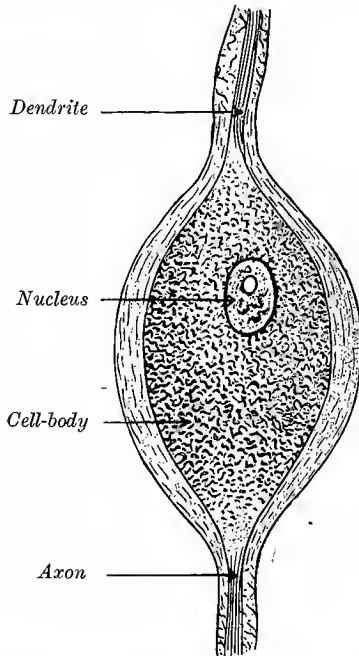


FIG. 11.—Pyramidal cell from the cerebral cortex of a mouse. (After Cajal.)

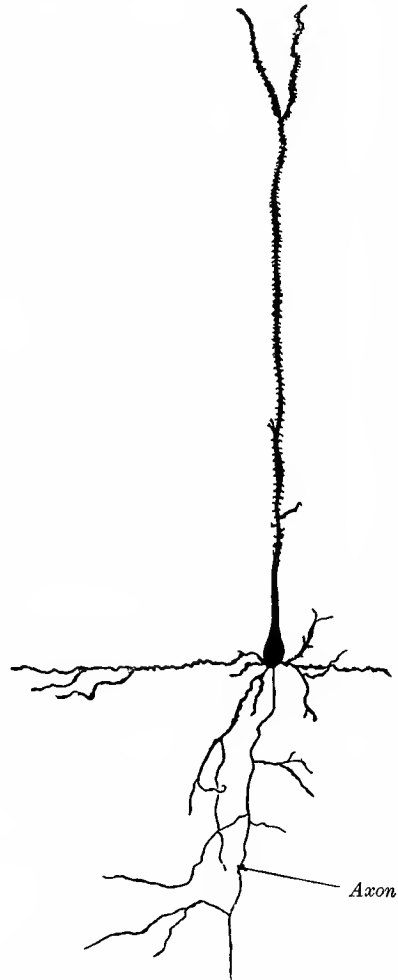
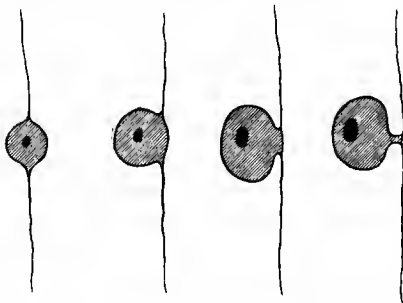


FIG. 10.—Diagram showing the manner in which a bipolar cell is transformed by unilateral growth into a unipolar form.



those connected with the organs of nutrition (sympathetic nervous system) and those belonging to peripheral sensory neurons. These aggregations of

nerve cells are bound together by connective tissue and form small irregular bodies called ganglia. Small isolated groups of nerve cells within the cerebro-spinal axis are usually designated by the term 'nuclei.'

Nerve Fibres.—The processes of the nerve cells are invested by sheaths to form nerve fibres. From their distribution these may be described as—

1. Peripheral, extending between the nerve cell and the body structures generally; the peripheral fibres are gathered into bundles held together by connective tissue, and constitute the peripheral or distributed nerves.

FIG. 12.—Cell of Purkinje from the cerebellum of a cat. (After Cajal.)

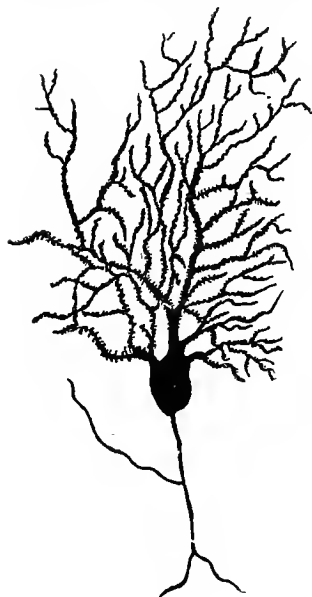
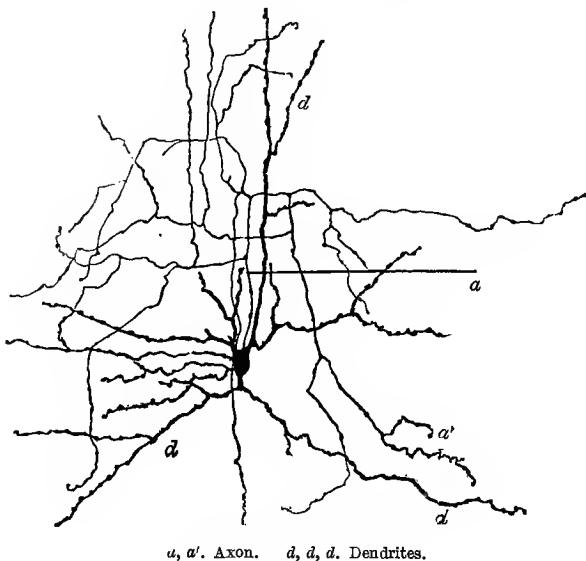


FIG. 13.—A multipolar cell of type II. from the cerebral cortex. (Cajal.)



a, a'. Axon. d, d, d. Dendrites.

2. Central, extending between the nerve cell and the deeper parts of the central nervous system; these make up the 'tracts' of the brain and spinal cord.

The essential component of each nerve fibre is the nerve cell process which forms the central core or axis cylinder.¹ It consists of a series of fine axis-fibrillæ extending along the whole length of the fibre and continuous with the

¹ Attention may be directed to the fact that, although the axis cylinders of sensory nerves are dendrites and of motor nerves are axons, no difference between them in structure can be made out, even with the microscope.

neurofibrillæ of the cell body (Fig. 14). The majority of the axis cylinders, are surrounded by a thick whitish fatty material known as the white substance of Schwann or medullary sheath. This substance is not uniformly continuous along the course of the fibre but is interrupted at regular intervals, which

FIG. 14.—Transverse and longitudinal sections of medullated nerve showing axis fibrillæ. (After Biedermann.)



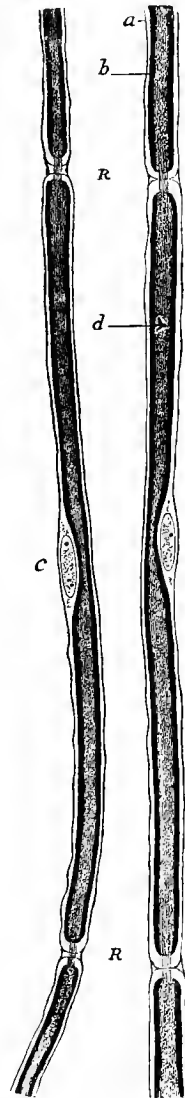
are known as the nodes of Ranvier (Fig. 15). Nerve fibres possessing the medullary sheath are spoken of as medullated fibres; they make up the greater part of the peripheral nerves and the tracts of fibres within the brain and spinal cord. Fibres belonging to the sympathetic nervous system are not sheathed by this substance of Schwann; they are, therefore, described as non-medullated fibres (Fig. 16). On the outside of the medullary sheath—or, in the case of a non-medullated fibre, forming the only covering for the axis cylinder—is a thin structureless membrane known as the neurilemma or primitive sheath of Schwann. It is a continuous sheath and is not interrupted at the nodes of Ranvier; each internodal portion, however, possesses a nucleus. There is no neurilemma round the nerve fibres in the cerebro-spinal axis.

At their extreme terminations all the nerve fibres lose their sheaths and end as naked axis cylinders.

Neuroglia.—The fibres and cells of the cerebro-spinal axis are held together by supporting cells termed neuroglia cells. These are spider-like in form, consisting of multangular cell bodies with numerous fibrillar processes which extend around and amongst the nerve cells and nerve fibres (Fig. 17).

Neuron Theory.—In the foregoing description the neurons have been referred to as independent morphological units—that is to say, each neuron is regarded as

FIG. 15.—Portions of two medullated nerve fibres.



a. Neurilemma.
b. White substance of Schwann.
c. Nucleus.
d. Axis-cylinder.
R, R. Nodes of Ranvier.

complete in itself and not continuous with any other neuron. Functionally, it is closely related to other neurons, but the relationship is one of contiguity, not continuity. The axon of one cell may form arborisations round another cell, or amongst the dendrites of this other cell, but there is no continuity of their protoplasm. The arrangement has been aptly compared to that of two trees growing alongside one another, with their branches intermingling and touching, but obviously not continuous.

This conception is usually termed the neuron doctrine. In recent years it has been strongly opposed by some observers. According to these the neurofibrillæ are continuous through the axis-fibrillæ from cell to cell, so that there is a continuous path from sensory surface to responsive mechanism. There seems to be little doubt that in some of the less highly specialised nerve mechanisms continuity can be demonstrated, but whether such continuity is universal must still be considered as undecided. The important facts for the psychologist are that there is functional continuity between neurons, and that each neuron is so closely associated with several other neurons that no part of the nervous system can be considered as separate from the rest.

FIG. 16.—A small nervous branch from the sympathetic system.



a. Two medullated nerve fibres among a number of non-medullated nerve fibres, b.

B. Physiology

The Nutritional Relations of Nerve Cells and Nerve Fibres.—According to the neuron theory the processes of the nerve cell are merely prolongations of the general protoplasm of the cell, and their vitality is dependent therefore on that of the neuron as a whole. Whether the theory be correct or not there is no doubt that the nerve cell exerts an important influence over the nutrition of its processes.

If a nerve fibre be cut across, the portion which is no longer in communication with the cell rapidly dies, is broken up, and then absorbed. The part still connected with the cell, except for a small distance from the cut surface, preserves its vitality during the life of the cell. If measures be taken to bring the cut ends of the nerve into apposition, even after a considerable period has elapsed, the nerve will regenerate by the growth of new fibres from the central stump, these fibres using the old pathways and growing down to the original terminations.

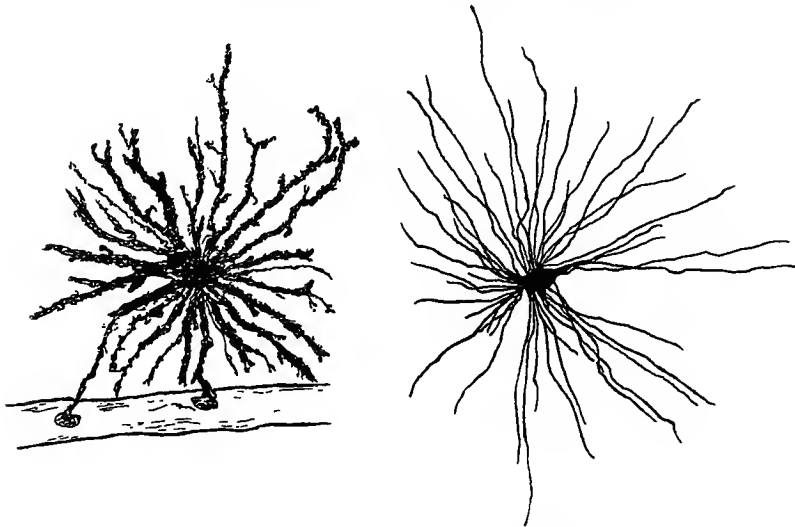
Until recently it was supposed that, after section of a nerve fibre, the nerve cell and its attached processes were unaffected. It is now known, however, that certain changes—as a rule temporary—take place in the nerve cell. The tigroid bodies are broken up and diffused throughout the cell (chroma-

tolysis) and the cytoplasm swells up. After a certain time (about eighteen days) the cell begins to recover its normal appearance, but occasionally no regeneration takes place.

The two main characteristics of a nerve fibre are its properties of (1) responding to a stimulus (excitability) and (2) conveying an impulse (conductivity).

Excitability of Nerve.—Normally, stimuli are received only at the terminal arborisations of the dendrites, and the impulse passes thence to the nerve cell and through it to the axon. Experimental investigation, however,

FIG. 17.—Neuroglia cells of brain. (After Andriezen.)



A. Cell with branched processes.

B. Spider cell with unbranched processes.

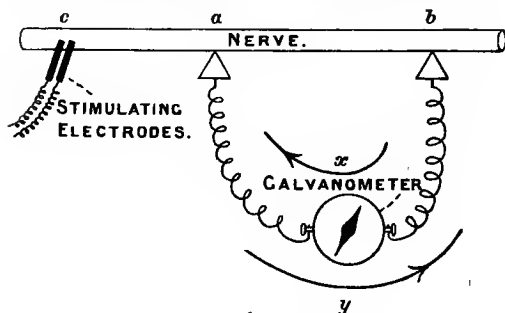
demonstrates the fact that the nerve fibres are excitable in any part of their course; chemical, mechanical, thermal, and electrical stimuli are all capable of starting an impulse in the nerve fibre, and this impulse is conducted along the fibre, producing effects very similar to those of the normal impulse. Of all forms of stimuli the electrical is the most convenient for experimental work, as the amount of stimulus can be readily controlled, and at the same time no appreciable damage is done to the nerve. In man the electrodes cannot of course be applied directly to the nerve, but the nerve can, with satisfactory results, be stimulated through the skin. This method is frequently used to investigate motor nerves; either the faradaic (alternating) or galvanic (continuous) current may be employed. One electrode of large diameter is

applied at some remote part of the skin surface, the other of smaller diameter is applied to the skin directly over the nerve under investigation.

A certain amount or intensity of stimulus is required to excite a nerve. The smallest stimulus sufficient to evoke the phenomenon is known as the minimal or threshold stimulus. In most cases increase in the strength of the stimulus up to a definite limit is followed by increased excitation, as indicated by a more marked response. The stimulus which gives the greatest response is the maximal stimulus, and, generally speaking, any increase beyond this is accompanied by a progressive decrease in the response.

Conductivity of Nerve.—The nerve cell and its processes, composed as they are of a highly specialised form of protoplasm, possess in great degree the capability of transferring impulses from point to point of their substance. Under normal circumstances these impulses are conveyed only in one

FIG. 18.—Scheme showing apparatus required for demonstrating the wave of negativity in a nerve.



direction, from dendrite to axon through the cell. By stimulating a nerve experimentally it can be shown, however, that the nerve can conduct an impulse in both directions, although in actual experience it is never called upon to do so.

Excitability and conductivity may both be modified by changes in temperature, by narcotic drugs, by the passage of an electric current, etc. As a rule both

properties are affected by the same agent but not necessarily to the same degree.

Electrical Changes in Nerve.—If two areas on a perfectly normal nerve be connected to a galvanometer it will be found that they are iso-electric, i.e. no current will flow through the circuit. When, however, an impulse traverses the nerve, definite electrical changes take place; the point which the impulse is passing at any particular instant becomes electrically negative to every other point on the nerve. This can be demonstrated by connecting up any two points (a and b, Fig. 18) to a galvanometer and then stimulating the nerve at c. When the impulse reaches a, this point becomes negative to b and a current passes through the galvanometer in the direction of the arrow x. The impulse leaves a and travels to b which then becomes negative and the current now passes in the reverse direction as indicated by the arrow y.

The great importance of this phenomenon, which is known as the wave of negativity, is that it always accompanies a nerve impulse, whether that impulse

be the normal one or due to experimental stimuli. Hence, if the presence of this wave can be demonstrated in a nerve, it is equivalent to demonstrating the passage of an impulse along the nerve. It will be evident that this is of the greatest service in estimating the transmission of impulses along sensory nerves, where the result is a sensation and not a mechanical response which could be observed.

The Nature of the Nerve Impulse.—The nerve impulse, which travels through the nerve cell and its processes, results from the action of some stimulus which has the power of liberating energy stored up within the protoplasm. Practically the only evidence of an actual liberation of energy from the material of the nerve fibre is the electrical change—the wave of negativity that passes along the nerve. The particular form which this energy takes is quite unknown. For a long time it was believed to be electrical but the measurement of its velocity easily disproves this. A nerve impulse travels at the rate of about 120 metres per second in man; this is exceedingly slow compared with the velocity of electricity or of light, but comparable with that of sound which is due to movements of a ponderable medium.

The passage of the nerve impulse has been likened to that of a spark along a train of gunpowder leading to a magazine. The essential difference is that the powder is completely destroyed in the process, while there is no apparent change in the nerve. If a nerve cell, however, be repeatedly stimulated diffusive changes become evident in the tigroid bodies (chromatolysis). There is no perceptible alteration in the axis-cylinder process, but this is supposed to be due to the fact that the axis-cylinder sheath, i.e. the white substance of Schwann and neurilemma, serves as a nutritive reservoir which rapidly replaces any material destroyed. The medullary substance has another function: it acts in a manner similar to that of the insulating material round an electric wire, and prevents the diffusion of the nerve impulse.

Nerve cells possess considerable powers in the direction of modifying the impulses which reach them. They may either reinforce an impulse or they may partially or completely block it; this latter effect is known as inhibition. They may collect weak impulses and combine them (summation) into one effective impulse; or in place of sending out one impulse as the result of a single stimulus they may send out several at more or less regular intervals (rhythmical impulses). All recent experiments tend to show that this last form is that generally accomplished by the nerve cells, and further that each nerve cell or group of nerve cells, has its own particular rhythm which remains unaltered whatever be the form of stimulus employed.

Specific Energy of Nerves.—A question of considerable interest to the psychologist is whether the impulses conveyed by different nerves are similar in nature. In other words, Is the nerve impulse to be compared to a current of electricity, the effect of which depends entirely on the mechanism with which it is connected, e.g. electric bell, electric light, etc.? The generally accepted belief,

and the one which accords best with experimental facts, is that the impulse in all nerves is identical in kind, although of course it may vary in intensity, the various responses being determined solely by the different terminations.

According to the opposite theory the impulse varies with the nature of the nerve, the character of the impulse being different in a sensory nerve from that in a motor nerve, etc.

Reflex Actions.—It has already been pointed out that the simplest working unit of the nervous system is made up of two neurons, one motor, the other sensory. When the peripheral terminations of the sensory neuron are stimulated, the impulse travels to the sensory cell, is transferred to the motor cell, passes down the efferent axon, and elicits a response in the associated motor mechanism. This response, which is quite involuntary, is known as a simple reflex action, and the pathway the impulse has traversed from sensory periphery to responsive mechanism is termed a reflex arc or pathway.

The whole nervous system consists of series of reflex pathways of various degrees of complexity, and it is important, therefore, that the student should clearly understand in the first instance the mechanism of the simpler forms. It may be stated at once that a simple independent reflex arc, consisting of only two neurons, does not exist in any of the higher forms of animal life. Each sensory neuron is connected not with one but with several motor neurons and frequently with several intermediate neurons.

Simple examples of reflex actions can be well studied in a frog, the brain of which has been destroyed: if, in such an animal, one toe be pinched the foot is immediately drawn away; even in this case it will be obvious that more than one muscle is thrown into action. In the human subject if an object suddenly approaches or touches the front of the eyeball, the eyelids rapidly close. This is known as the winking reflex, and is an example where a single muscle (composed, however, of many muscle fibres) is brought into play. This reflex demonstrates also the fact that, although the movement is involuntary, it may be associated with consciousness. Similarly, if the sole of the foot be tickled, whether the individual be awake and conscious, or asleep and unconscious, the leg is drawn up.

The simple reflex pathway consisting of two neurons is useful as a theoretical starting-point from which to study certain properties of reflexes. For the performance of a reflex action a measurable period of time is required; this is known as the reaction time and is calculated from the time of application of the stimulus till the commencement of the response. A portion of this time is taken up by the transmission of the impulse along the nerves, and this portion can be calculated since the velocity of nerve impulses is known and the length of the arc can be measured. In every case, however, even when to this transmission time are added the latent periods of the receiving and responding mechanisms, the total is less than the reaction time. Time, therefore, is lost somewhere in the course of the reflex arc, and this may occur either in the cell

bodies, in the finer processes, at the junction of the sensory with the motor neuron, or at all of these ; in other words a certain amount of time is taken up in the reflex centre, and this is described as the reflex time or the reduced reaction time.

It has already been pointed out that the nerve cells may considerably modify impulses passing along their processes, and one important fact of this nature, specially related to the activity of the reflex centre, is that the reflex response to a stimulus does not cease immediately after the stimulus has ceased to act but may persist for some time.

In the higher types of reflex, where each sensory neuron is connected with several motor neurons, an entering peripheral impulse may put into action many responsive mechanisms. Indeed so closely interrelated are all the neurons that a single sensory impulse is theoretically capable of affecting all the motor cells of the central nervous system. That this conception is not entirely hypothetical is seen in cases of strychnine poisoning where the excitability of the neurons is greatly increased. In such cases the slightest stimulus, such as a faint noise, a draught of air, etc., suffices to throw the patient into general convulsions.

It is apparent then that an entering impulse must select definite paths amongst the network of interlacing fibres. Certain of these paths are determined in the lower forms of animal life as accumulated experiences of the most satisfactory reflex arcs absolutely essential to the preservation of existence, e.g. the reflexes which control the circulation and respiration. Other paths have been developed first as conscious habits ; when the habit is fully established the element of consciousness sinks into the background, and, if brought forward at any subsequent time, proves a hindrance rather than a help ; for example the awkward gait of an individual who is conscious of the fact that his method of walking is under observation.

In considering the complex type of reflex pathway, another action of the reflex centre becomes apparent. If a decapitated frog be suspended so that the limbs hang free, and areas on the skin be stimulated (usually by the application of small pieces of paper soaked in an irritant), purposeful efforts are made by the limbs to remove the stimulant. This necessitates the presence of some arrangement, independent of the brain, by which orderly, intentional movements can be carried out. Since the sensory arm of the arc communicates with several motor neurons, it follows that every motor neuron is brought under the influences of several sensory paths. Hopeless confusion and disorder in muscular movements is prevented by the power which the reflex centre has of inhibiting (i.e. blocking) certain pathways. In the ordinary reflex, therefore, only such impulses are allowed to pass as will produce an orderly response ; hence these reflexes are designated co-ordinated reflexes.

To indicate briefly how closely interrelated are the groups of neurons, and how delicately balanced, two easily demonstrable reflex phenomena may be

cited : (1) a simple reflex may be the starting point for a succession of co-ordinated movements, e.g. the swallowing reflex, where a mass of food is driven down to the stomach by a series of regular progressive contractions of the gullet ; (2) if the sole of the foot of a sleeping person be tickled, the leg is drawn up and after an interval is again straightened out. The return to the straight position is not merely a passive falling back of the limb but is an orderly movement, showing that the first reflex has initiated a second reflex producing an opposite effect. A similar phenomenon occurs in the reflex movements of ordinary walking.

CHAPTER III

THE GENERAL CONSTRUCTION AND DEVELOPMENT OF THE NERVOUS SYSTEM

As animals ascend in the scale of organisation from the simplest types they assume a bilateral symmetry which, however, is seldom rigidly adhered to. Speaking generally, the external protective and supporting (somatic) structures are similar on the right and left sides of the body ; the internal (visceral

FIG. 19.—Human embryo—length 2 mm.
Dorsal view. (After Graf Spee.)

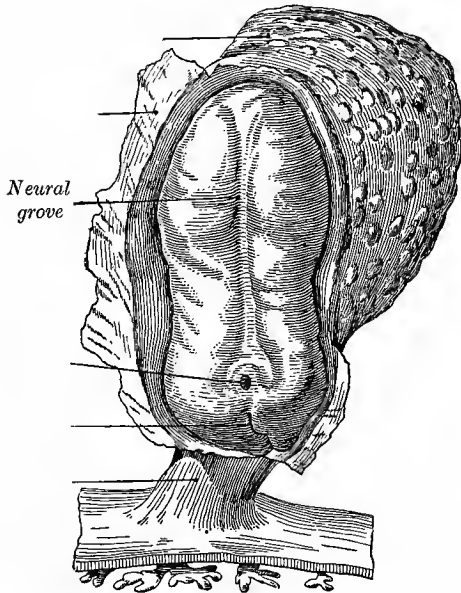
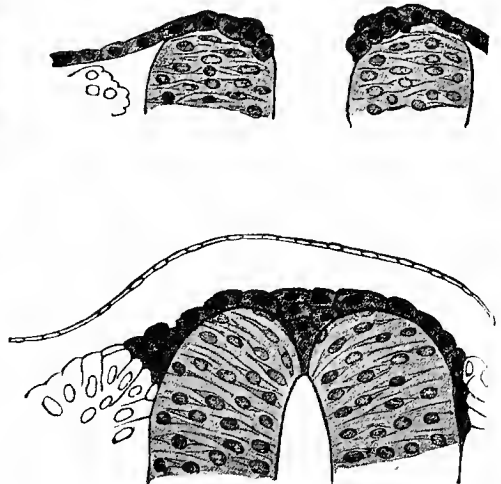


FIG. 20.—Two stages in the development of the neural crest in the human embryo. (Lenhossék.)

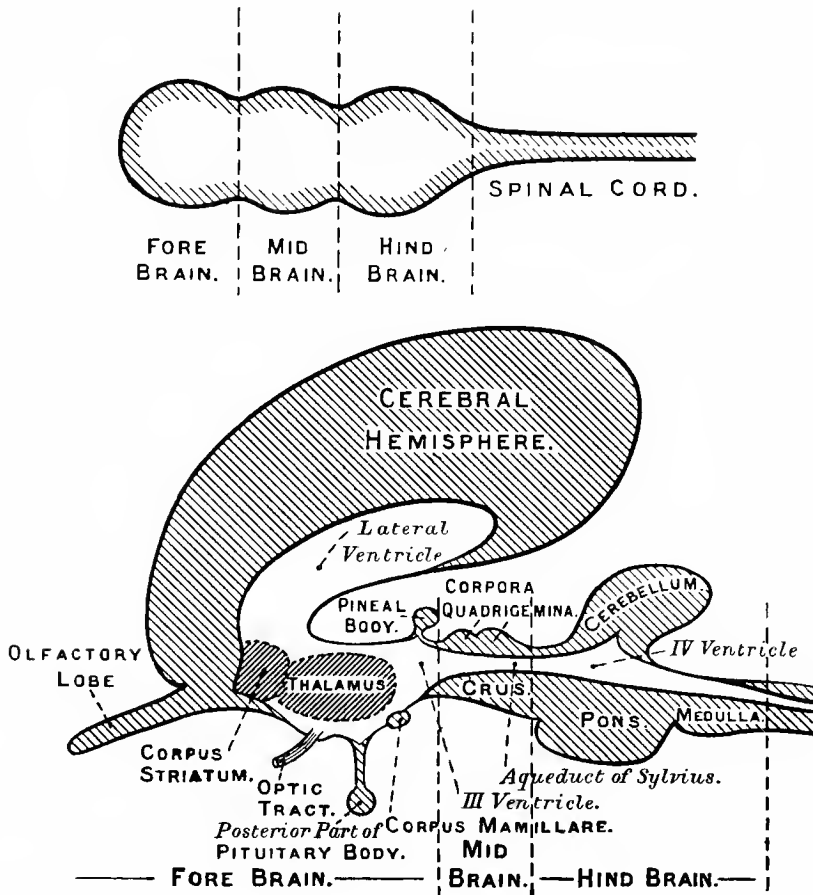


organs of nutrition, etc., rarely show complete symmetry. In addition, as is strikingly seen in worms, the animal is built up of a series of transverse discs or segments, many of which are similar to one another ; each contains all the organs essential to life, and, in some animals, is capable of independent existence. In the higher forms bilateral symmetry and transverse segmentation

are still evident except in the visceral system ; in the head the transverse segmentation is very obscure.

These factors influence the form which the nervous system ultimately assumes. To meet the requirements of the transverse segmentation of the

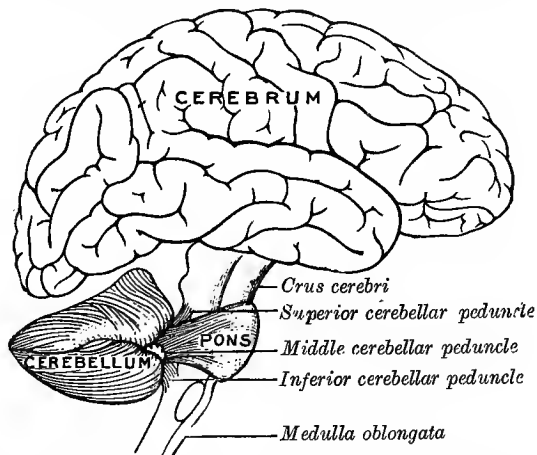
FIG. 21.—Diagram showing the chief structures developed from the three original brain vesicles.



body the nervous system is also segmented, i.e. each body segment contains its own group of neurons. For facility of inter-communication and for protection, the cell bodies of the neurons are grouped together into ganglia and are withdrawn from the surface. Each segment, being bilaterally symmetrical, contains a right and a left ganglionic mass. In many circumstances it is

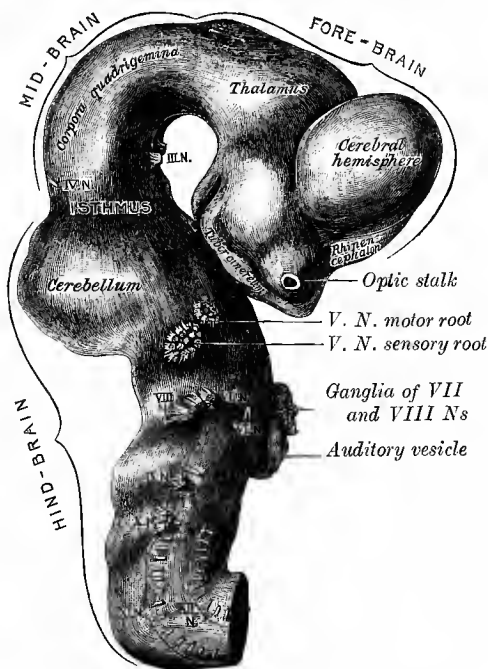
advantageous for the segment to respond as a whole to external stimuli; this is effected in the first instance by cross communications (commissures) between the ganglionic masses, and at a later stage of evolution by the fusion of the two masses into one. Similarly, when the body segments join together and lose their individuality, these ganglionic masses also fuse, and a long median column of nerve cells and fibres results. From this column nerve fibres come off in bundles corresponding to the original segments.

FIG. 22.—Scheme showing the connections of the several parts of the brain. (After Schwalbe.)



Primitively each segment is capable of only simple reflex actions. As the segments combine the reflexes become more intricate and each increase in intricacy renders more necessary the establishment of a common co-ordinating nerve centre. The head end of the nervous column takes on this complicated function and is differentiated as the brain. Another factor in increasing the complication of the brain is the great concurrent increase in development of the special sense organs, the impulses from which have all to be co-ordinated and transferred to the proper responsive mechanisms.

FIG. 23.—Exterior of brain of human embryo of four and a half weeks. (From model by His.)



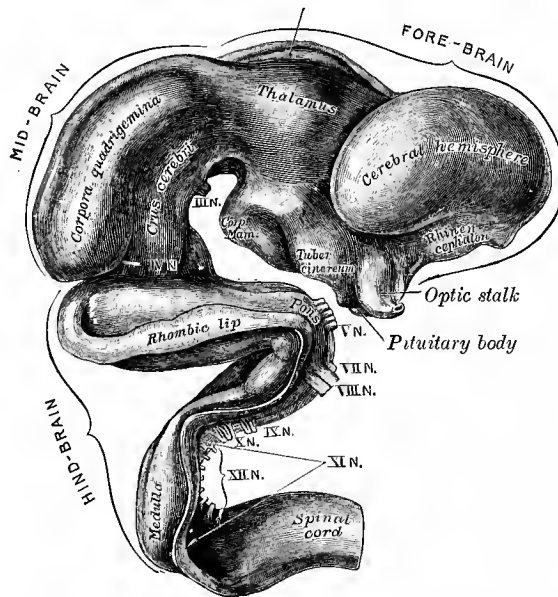
Development of the Central Nervous System. — In vertebrate embryos at a very early stage the central nervous system is laid down as a median neural groove on the dorsal surface (Fig. 19). By the upgrowth

Development of the Central Nervous System. — In vertebrate embryos at a very early stage the central nervous system is laid down as a median neural groove on the dorsal surface (Fig. 19). By the upgrowth

and fusion of the lips of this groove a long neural tube results. Along either lip of the neural groove is a prominent thickening termed the neural crest; when the lips fuse a wedge-shaped ridge is formed along the line of closure (Fig. 20).

As development proceeds, the neural tube is cut off from the general covering layer of the embryo by the growth round it of the skeleton of the vertebral column and skull. The head end of the neural tube dilates to form three

FIG. 24.—Exterior of brain of human embryo of five weeks.
(From model by His.)



bulbs or vesicles, the fore-brain, mid-brain, and hind-brain vesicles respectively (Fig. 21), which are ultimately modified to form the brain, while the rest of the tube becomes the spinal cord. The development of these portions need not be considered in detail; it will be sufficient to indicate the main modifications which they undergo (Figs. 21–26).

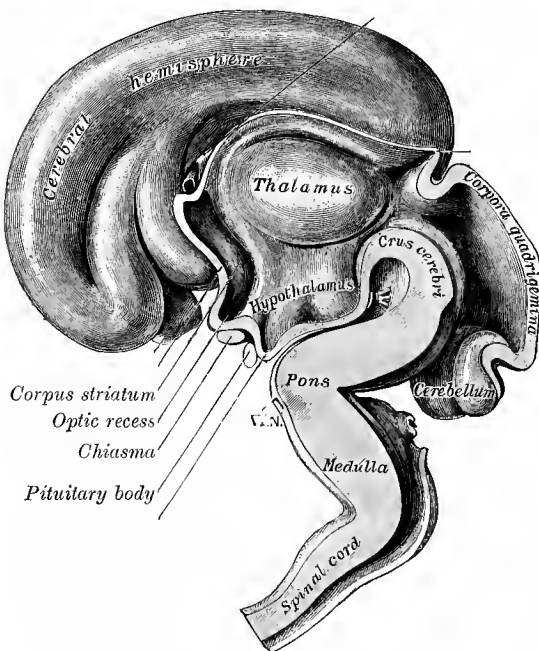
Spinal Cord.—The nerve cells accumulate round the canal of the neural tube to form what is known, from its colour, as the grey matter of the cord. On the periphery of the grey matter, nerve fibres are grouped into tracts; these fibres at a later stage acquire white medullary sheaths and form the white matter of the cord. The original canal of the tube persists as the central canal of the cord.

Hind-brain.—From the back part of the floor of the hindmost vesicle the

medulla oblongata or bulb, continuous with the spinal cord, is formed, and in front of this the pons Varolii develops. In the roof the cerebellum or little brain appears. The dilated cavity of the vesicle is termed the fourth ventricle.

Mid-brain.—In the floor of the middle vesicle the crura cerebri or peduncles of the brain are laid down. The roof of the vesicle develops four prominences

FIG. 25.—Median section of brain of human embryo of three months. (From model by His.)



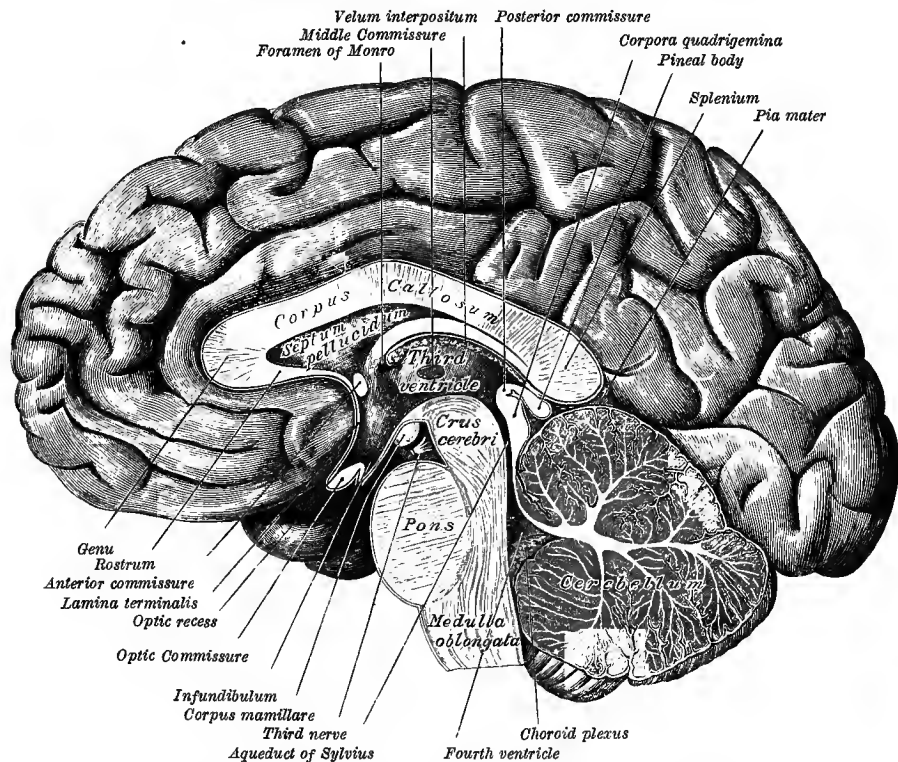
called the corpora quadrigemina; in fishes, amphibians, reptiles, and birds there are but two of these prominences and they are known as the optic lobes. The cavity of the vesicle remains as a narrow channel, the iter, or aqueduct of Sylvius.

Fore-brain.—It is in the foremost vesicle that the most complex changes take place. The cavity of the posterior half of the vesicle dilates to form a vertical slit-like space—the third ventricle—which communicates behind with the fourth ventricle through the aqueduct of Sylvius. From the back part of the roof a small evagination develops into the pineal body which in some of the lower animals, e.g. lizards, forms the rudimentary pineal eye.

In either lateral wall of the third ventricle large numbers of nerve cells

accumulate to form a grey mass known as the thalamus. On either side a portion of the floor is evaginated in the form of a hollow bulb with a narrow stalk. The bulb is ultimately modified to form the retina—the portion of the eye which receives the stimulation of light; the stalk becomes solid and forms the optic tract and nerve. From the centre of the floor a downward evagination takes place: an evagination from the lining of the upper part of the primitive mouth grows up to meet it; this is cut off later from its site

FIG. 26.—Medial antero-posterior section of adult human brain.



of origin, fuses with the median downgrowth from the third ventricle, and the two together form the pituitary body. Immediately behind this in the floor two little spherical bodies, lying side by side and known as the corpora albicantia or corpora mamillaria, are differentiated.

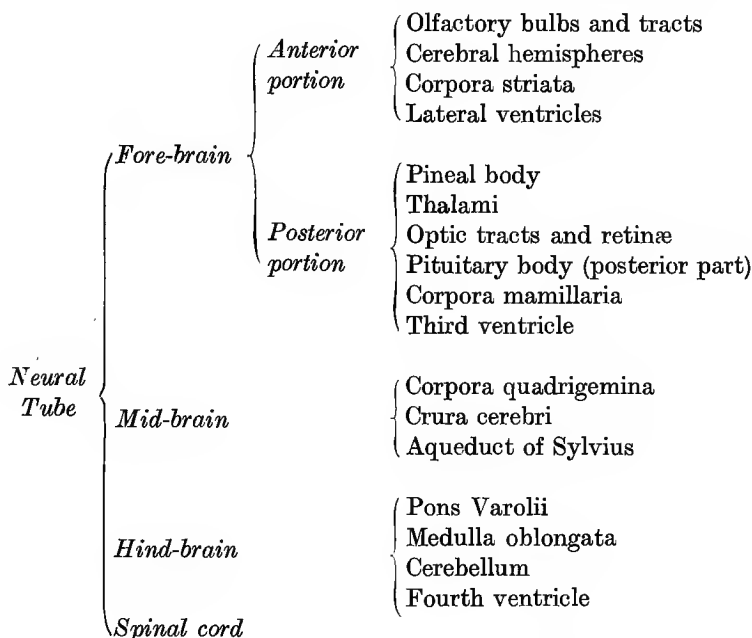
From the anterior half of the fore-brain vesicle four hollow outgrowths take place—two on either side. The first two are more or less cylindrical; they become completely solid as they grow and ultimately form the olfactory bulbs and tracts—structures concerned in the sense of smell. The other pair

form the cerebral hemispheres which grow at a rapid rate and finally greatly exceed in size all the other parts of the brain. Into them the original cavity of the vesicle is continued on either side as a triradiate diverticulum. These two diverticula are termed the lateral ventricles (right and left); they communicate with each other and with the third ventricle through a Y-shaped foramen—the foramen of Monro.

The cerebral hemispheres are brought into communication with one another by transverse strands of fibres known as commissures; the greatest of them is a broad transverse band called the corpus callosum.

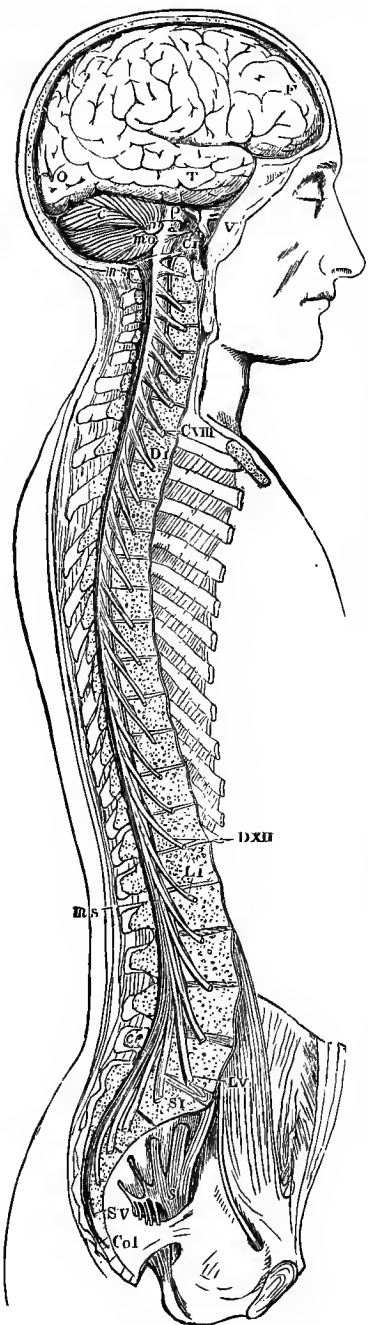
In the wall of each lateral ventricle, forming a swelling projecting into its interior, is a large mass of grey matter termed the corpus striatum.

The main modifications of the original neural tube may be thus summarised :



In the brain the grey matter is not, like that of the cord, entirely arranged in a regular mass round the central canal. A certain amount of it does lie in the walls of the brain cavities, but separate portions exist at intervals amongst the white fibres. In addition, the surfaces of the cerebral and cerebellar hemispheres are covered with grey matter.

Peripheral Nervous System.—The peripheral nervous system comprises all the distributed nerves and the ganglia in their course. It may be resolved into two secondary systems :



(A) the somatic system, the nerves of which run to the protective and supporting structures of the body,

(B) the sympathetic system distributed to the organs of digestion, respiration, and circulation.

(A) **The Somatic System.**—The somatic nerves are classified in two groups, (a) spinal and (b) cerebral or cranial, according to the portion of the skeleton from which they emerge. The spinal nerves pass out from the sides of the vertebral column between adjacent vertebræ. The cerebral nerves find exit through holes in or between the bones forming the base of the skull.

Spinal Nerves.—In man there are thirty-one pairs of spinal nerves named from the regions of the vertebral column where they emerge (Fig. 27) thus :

8 Cervical	= neck region.
12 Thoracic	= region of chest.
5 Lumbar	= region of loins.
5 Sacral	} = terminal portion of
1 Coccygeal	
	vertebral column.

Every spinal nerve is attached to the spinal cord by two roots : one to the front of the cord, containing the motor fibres, is termed the anterior root, the other to the back of the cord, consisting chiefly of sensory fibres, is designated the posterior root. The two roots join together at a short distance from the cord and form a complete spinal nerve. The roots can be readily distinguished from one another by the fact that there is a little swelling on the posterior root due to the presence in it

FIG. 27.—General view of the cerebro-spinal axis.
(After Bourguery.)

O. T. F. on cerebral hemisphere. C. cerebellum. P. pons. *mo.* behind medulla. *ms.* end of spinal cord. O I to O VIII. Cervical nerves. D I to D XII. Thoracic nerves. L I to L V. Lumbar nerves. S I to S V. Sacral nerves. Co I. Coccygeal nerve.

of a ganglion—the spinal ganglion; the anterior root is non-gangliated (Fig. 28).

The nerve cells of the spinal ganglia have single processes bifurcating in a T-shaped manner; one limb of the bifurcation (the dendrite of the cell) passes out to the complete spinal nerve, the other limb (the axon) runs into the spinal cord. The fibres in the anterior root are the axons of cells located in the grey matter of the spinal cord.

DEVELOPMENT.—The motor roots are formed as outgrowths from nerve cells in the anterior part of the neural tube. The fibres of the posterior root grow out from the cells of the spinal ganglia. These ganglia arise from the neural crest in the following manner: in each segment the cells of the crest increase rapidly in numbers and then migrate outwards forming thus a series of oval-shaped masses. The central processes of the cells grow inwards to the cord and the peripheral outwards to join the motor root.

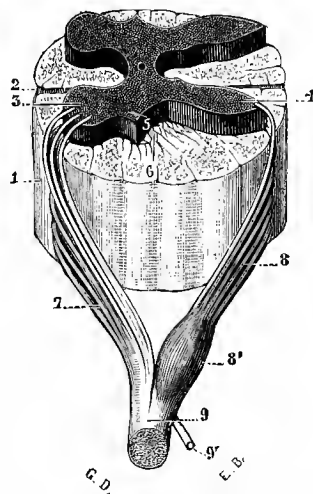
Cerebral (cranial) Nerves.—The cerebral nerves do not exhibit the regular segmental arrangement of the spinal nerves, neither are they regularly constituted of two roots—motor and sensory. Some are entirely motor, others purely sensory, and a few are mixed (Fig. 29).

In man twelve pairs of cranial nerves are recognised. The first and second pairs differ from all the other peripheral nerves in that, developmentally, they are really outgrowths of the brain substance. The names and general functions of the cerebral nerves are as follows:

- I. Olfactory (*s.*), connected with the organ of smell.
- II. Optic (*s.*), connected with the organ of sight.
- III. Oculo-motor (*m.*), to certain muscles of the eyeball.
- IV. Trochlear or pathetic (*m.*), to a muscle of the eyeball.
- V. Trigeminal or trifacial (*s., m.*), sensory to face and tongue, motor to muscles of mastication.
- VI. Abducent (*m.*), to a muscle of the eyeball.
- VII. Facial (*s., m.*), sensory to tongue, motor to muscles of expression.

(*s.*) sensory, (*m.*) motor.

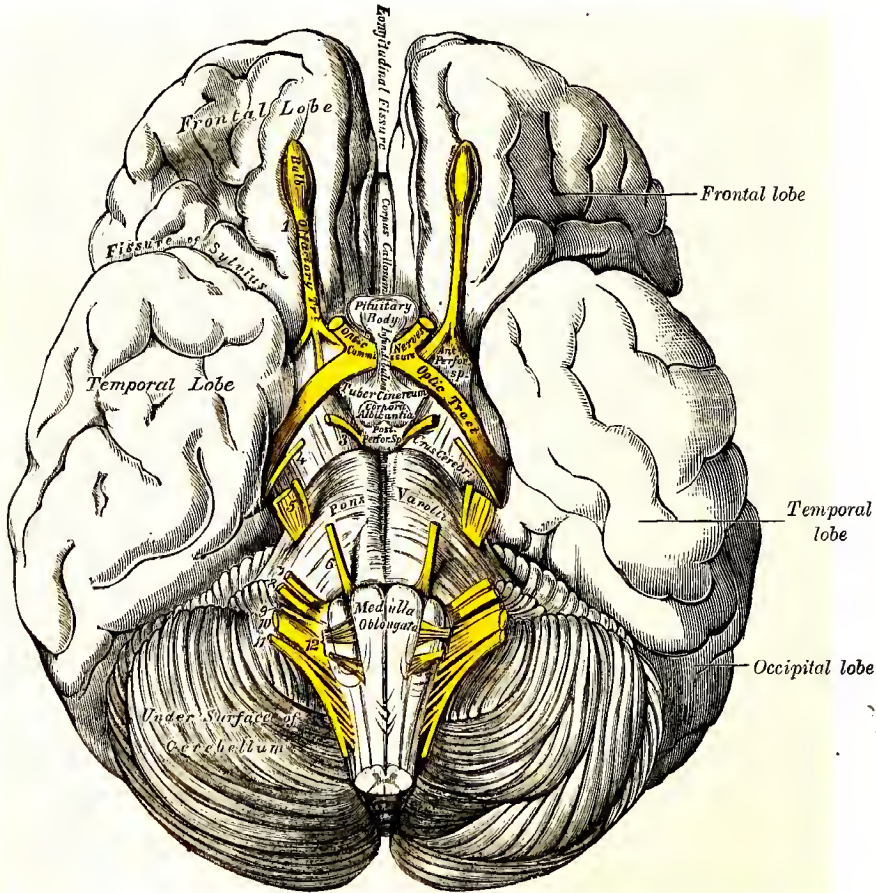
Fig. 28.—A spinal nerve with its anterior and posterior roots. (Testut.)



1. A portion of the spinal cord viewed from the left side. 2. Anterior median fissure. 3. Anterior horn. 4. Posterior horn. 7. Anterior root. 8. Posterior root, with 8', its ganglion. 9. Spinal nerve.

- VIII. Auditory (*s.*), connected with the organ of hearing.
 - IX. Glossopharyngeal (*s., m.*), to tongue and pharynx.
 - X. Pneumogastric or vagus (*s., m.*), to the viscera.
 - XI. Spinal accessory (*m.*), a portion joins the vagus ; the other portion supplies two muscles of the neck.
 - XII. Hypoglossal (*m.*), to muscles of the tongue.
- (*s.*) sensory, (*m.*) motor.

FIG. 29.—Under surface of the brain showing the emerging cerebral nerves.



(B) **The Sympathetic System.**—The nerve cells connected with the organs of nutrition i.e. organs of digestion, of circulation, and of respiration, present an interesting variation from those belonging to the supporting and protective

Superior cervical ganglion of sympathetic

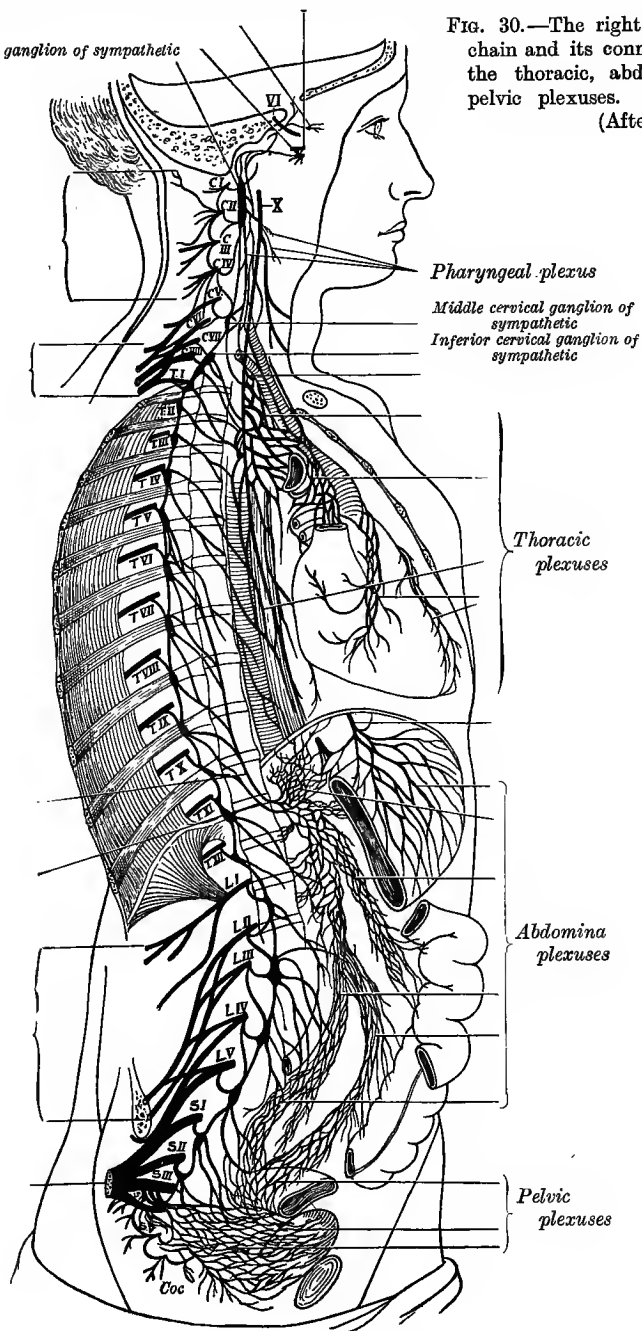


FIG. 30.—The right sympathetic chain and its connections with the thoracic, abdominal, and pelvic plexuses.

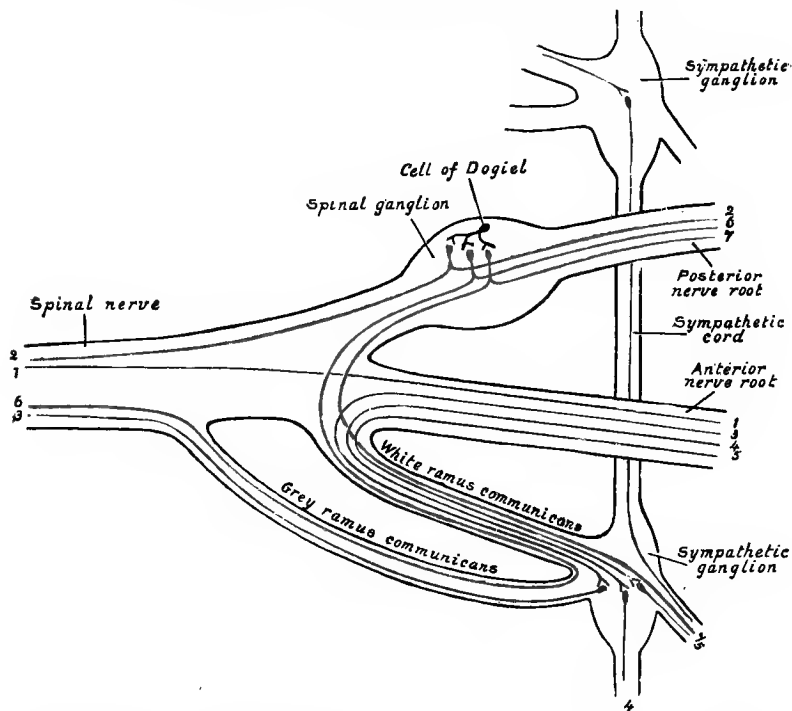
(After Schwalbe.)

mechanisms. Their withdrawal from the organs to a central axis is incomplete, small ganglia being present in the walls of the organs and along the pathways of their nerves towards the brain and spinal cord (Fig. 30).¹

For practical purposes the ganglia may be grouped into four series :

- (1) Peripheral ganglia, embedded in the viscera.
- (2) Irregular groups of ganglia associated with large sympathetic nerve plexuses in the thorax and abdomen.

FIG. 31.—Scheme showing structure of a typical spinal nerve.



1. Somatic efferent. 2. Somatic afferent. 3, 4, 5. Sympathetic efferent. 6, 7. Sympathetic afferent.

(3) The lateral ganglionic chains.

(4) The sympathetic nerve cells in the brain and spinal cord.

The lateral ganglionic chains are composed of small ganglia linked by fibres to adjacent ganglia. They extend, on either side of the vertebral column, from the base of the skull to the end of the column, and each ganglion is connected to a spinal nerve by communicating branches (rami communicantes). If the

¹ Although this may be regarded as the story of the evolution of these ganglia, yet during their actual development in the embryo the nerve cells forming them travel outwards from the neural crest to the regions where they are ultimately found.

segmental arrangement of these ganglia were as regular as that of the spinal nerves then every spinal nerve would have one ganglion connected with it. In the thoracic region and to a lesser extent in the lumbar and sacral regions, this arrangement is found ; in other regions, adjacent ganglia have fused with one another so that one ganglion may be connected with several spinal nerves. In the cervical region, for instance, there are three ganglia on either side instead of eight ; the uppermost is made up of four ganglia fused together, and each of the others similarly consists of two.

Typically two rami communicantes connect a sympathetic ganglion with a spinal nerve. The two rami differ slightly from one another in colour ; one is termed the white ramus communicans, the other the grey ramus communicans. The white ramus consists chiefly of medullated fibres which give the white colour to the ramus ; they are fibres which emerge from the spinal cord and pass to the ganglion. The grey ramus is composed chiefly of non-medullated fibres which originate as axons of cells of the sympathetic ganglion and run out to join the spinal nerve (Fig. 31).

Structure of a Complete Spinal Nerve.—The nerve fibres running to and from the supporting and protective structures are usually designated somatic in contradistinction to the sympathetic or visceral fibres to the organs of nutrition. A complete spinal nerve contains fibres from all the neurons essential to a complete nervous system, i.e. the fibres necessary for four reflex pathways namely :

- I. A somatic sensory motor arc.
- II. A sympathetic sensory motor arc.
- III. A somatic sensory sympathetic motor arc.
- IV. A sympathetic sensory somatic motor arc.

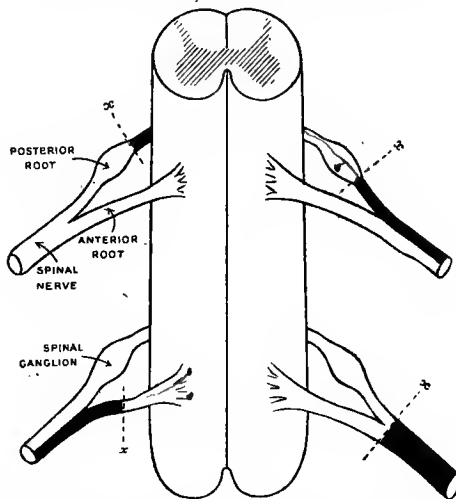
Unfortunately the sympathetic system is very difficult to study both anatomically and experimentally so that many of its precise interactions are still problematical. Thus it is yet doubtful whether the sympathetic system can carry out a reflex action without the interposition of the cerebro-spinal system ; and, further, the exact connections of the afferent fibres from the viscera are but imperfectly understood.

Methods of tracing the Course of the Nerve Fibres within the Spinal Cord and Brain.—If a cut surface of the spinal cord or brain be examined, no differentiation of the various tracts of nerve fibres can be made out, and special methods have therefore to be adopted in order to demonstrate them. The two chief methods may be indicated.

(1) *Embryological.*—The white sheaths of the medullated nerves are not acquired until some time after the nerve fibres have developed ; and what is important in this connection is that the different tracts of nerve fibres obtain their sheaths at different periods. By examining, therefore, a series of spinal cords or brains at different stages of embryonic life, individual tracts may be recognised.

(2) *Wallerian Degeneration*.—It has already been pointed out that if a nerve be severed the fibres which are cut off from their nerve cells undergo degeneration. This degenerative change is usually referred to as Wallerian degeneration, after Waller who first described it. By treating the spinal cord or brain with special stains, the degenerated fibres can easily be traced in

FIG. 32.—Diagram showing the portions of the spinal nerves that undergo degeneration after section.



x, indicates the line of the cut. The blackened portions are the parts that degenerate.

microscopic sections. When the degeneration takes place below the injury it is termed descending degeneration, and the tracts affected are called descending tracts; similarly degeneration above the injury is designated ascending, and the tracts ascending tracts (Fig. 32).

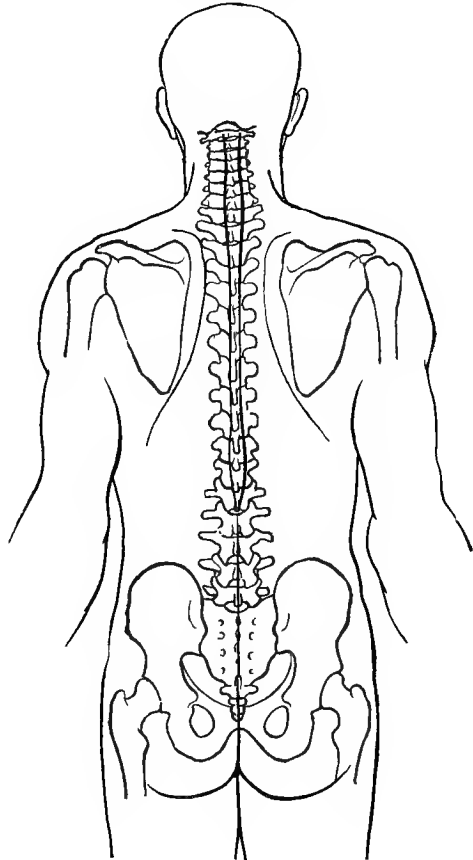
In animals injury to the nervous system may be produced experimentally, but in man observations must be conducted in cases where accidental injuries have occurred or where certain diseases have destroyed nerve cells in some known region of the brain or spinal cord.

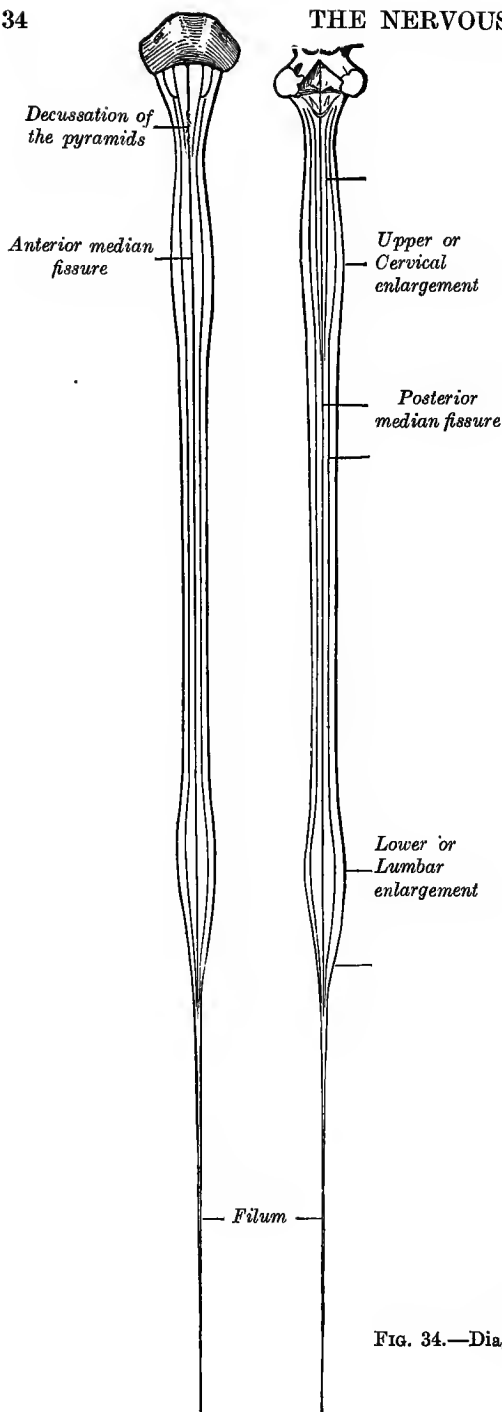
CHAPTER IV

THE SPINAL CORD

IN man the spinal cord is a long cylindrical structure lying within the vertebral or spinal canal. At the level of the joint between the vertebral column and the skull the spinal cord is continuous with the brain. Below, the functionally active part of the cord terminates somewhat abruptly in a conical extremity at the upper part of the lumbar region, i.e. it occupies about the upper two-thirds of the spinal canal (Fig. 33); a fine non-nervous strand however—the filum terminale—continues the cord to near the end of the vertebral column. Two enlargements disturb the regular cylindrical form of the cord (Fig. 34): one in the upper part where the large nerves to the arms are given off; the other at the lower end where the nerves to the legs emerge. Along the front of the cord is a well-marked longitudinal groove termed the anterior median fissure; an extremely narrow and shallow longitudinal groove—the posterior median fissure—similarly extends down the back of the cord. The relative depths of these two fissures are most clearly evident in a transverse section of the cord; in such a section it will be seen that a septum of neuroglia (the posterior

FIG. 33.—Showing the relation of the spinal cord to the dorsal surface of the trunk. The vertebræ, etc., are outlined in red.





median septum) extends nearly to the middle of the cord from the posterior median fissure (Fig. 35).

Although on superficial inspection the cord appears to be a solid structure, yet on careful examination, a fine canal will be found running down its centre; this, the central canal of the cord, indicates the original development of the cord from a tube.

At regular intervals the spinal nerves emerge from the sides of the cord, each nerve, as already described, coming off by two roots, a posterior sensory gangliated, and an anterior motor non-gangliated.

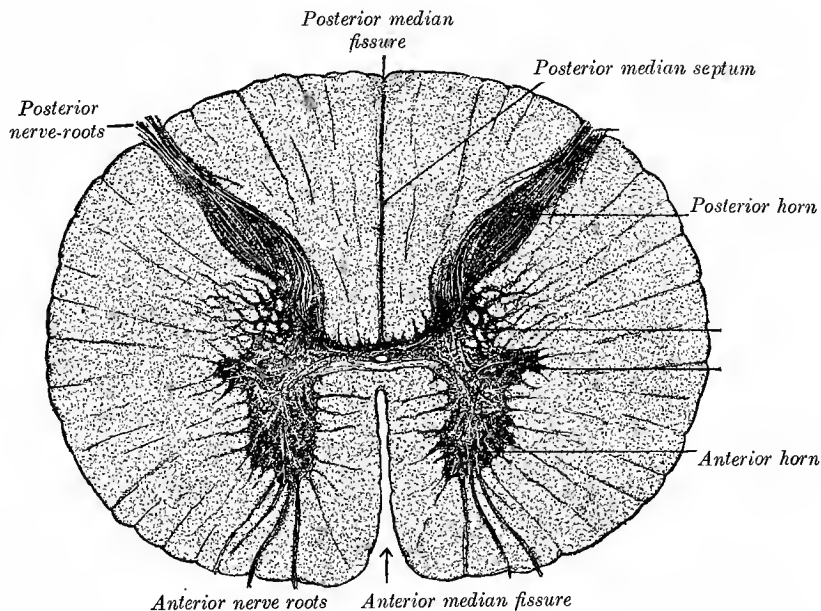
The cord is enveloped by three membranous sheaths. The innermost, known as the pia mater, is closely applied to the surface of the cord and carries its bloodvessels. It is separated by a space—the subarachnoid space—from the next membrane, the arachnoid, which is thin and delicate; the subarachnoid space communicates with the ventricles of the brain and through these with the central canal of the cord, and contains a fluid known as the cerebro-spinal fluid. The outermost membrane forms a tough fibrous covering and is called the dura mater; it is separated from the arachnoid by a fine capillary space—the

FIG. 34.—Diagrams of the spinal cord.

subdural space—which is moistened with lymph. To avoid repetition it may be pointed out here that the same three membranes are continued over the surface of the brain.

The substance of the cord is made up of nerve cells and nerve fibres supported by neuroglia ; the nerve cells are massed together around the centre and constitute the grey matter ; most of the nerve fibres are medullated, and are grouped into large tracts on the periphery of the grey matter to form the white matter of the cord.

FIG. 35.—Transverse section of the spinal cord in the mid-thoracic region.

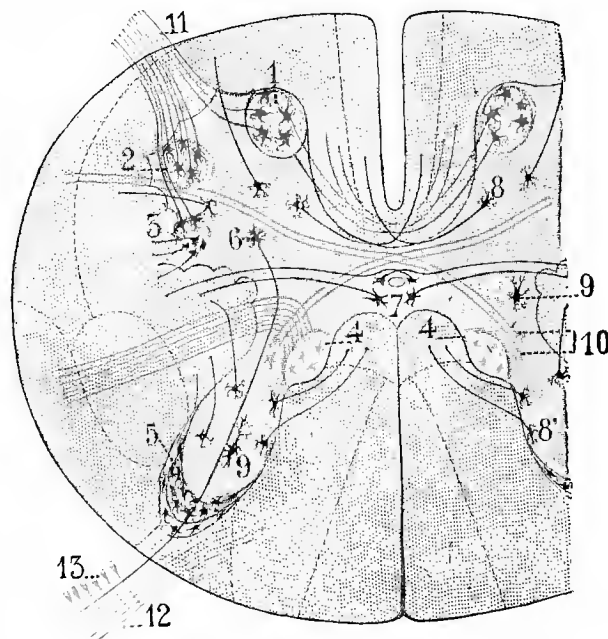


Grey Matter.—If a thin transverse section of the spinal cord be examined under the microscope it will be seen that the central grey material assumes roughly the form of the letter H. The transverse bar contains the central canal, and serves to connect the parallel limbs to one another ; it is known as the grey commissure. In each of the lateral limbs an anterior and a posterior part are recognised. The anterior portion, which is somewhat bulbous in shape, is termed the anterior cornu or horn : the axons of the majority of its cells are the nerve fibres forming the anterior or motor root of the spinal nerve ; from other groups of cells the efferent sympathetic fibres emerge (Fig. 36).

The posterior portion, called the posterior cornu or horn, tapers towards its extremity which is near the periphery of the cord ; the cells which it contains have, for the most part, short axons which arborise round the anterior

horn cells of its own or of the opposite side, either in its own or in neighbouring segments. A special group of nerve cells situated at the base of the posterior horn differs from these in possessing long axons which run into the white matter and thence towards the brain, in a manner to be presently described. This collection of cells forms a long column known as the column of Lockhart Clarke.

FIG. 36.—Mode of distribution of the nerve cells in the grey matter. (Schematic.)
(Testut.)



1, 2, 3, 6, 8. Nerve cells in anterior horn. 4, 4. Column of Clarke. 5, 8', 10. Other cells in posterior horn.
9. Multipolar cells of type II. 11. Anterior root. 12. Posterior root. 13. Spinal ganglion.

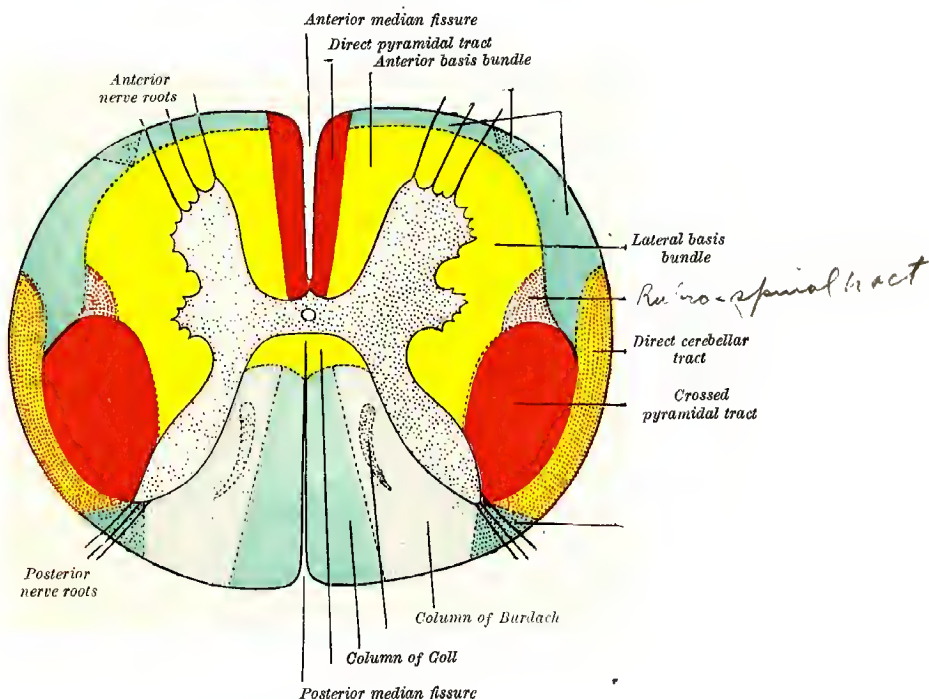
White Matter.—The tracts of nerve fibres in the white matter may be divided either: (1) anatomically—into short and long tracts, or (2) physiologically—into ascending and descending tracts. The short tracts lie immediately adjacent to the grey matter, along its outer side and round the anterior horn; they form the antero-lateral basis bundles. The fibres which constitute them run for varying distances from one part of the cord to another, some connecting adjacent segments, others running comparatively long distances in the cord. Some of the fibres convey impulses upwards, others downwards (Fig. 37).

The long tracts extend between the brain and spinal cord. Those which convey impulses upwards towards the brain are termed ascending tracts—

they are mainly sensory ; conversely, the descending tracts carry impulses downwards in the cord and are largely motor. There are several minor tracts belonging to this series, but it will be sufficient to indicate the more important ones, viz. :—

- | | | |
|------------|---|-----------------------------------|
| Descending | . | { Direct pyramidal tracts. |
| | | { Crossed pyramidal tracts. |
| Ascending | . | { Columns of Goll and of Burdach. |
| | | { Direct cerebellar tracts. |

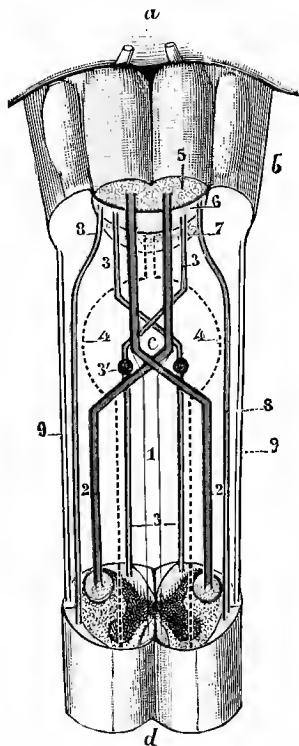
FIG. 37.—Diagram of the tracts in the spinal cord. References are given only to the tracts described in the text.



Pyramidal Tracts.—The pyramidal tracts are the axons of nerve cells situated in the surface or cortex of the cerebral hemispheres. They extend down through the brain, one on either side, till they reach the medulla where they undergo partial decussation. One portion of each tract crosses to the opposite side and runs down in the lateral part of the cord between the anterior and posterior horns as the crossed pyramidal tract. The remainder of each tract passes down on its own side on the mesial aspect of the anterior horn

as the direct pyramidal tract (Fig. 38). A number of the fibres of this tract cross to the opposite side in each segment, so that by the time the end of the tract is reached all the fibres have crossed to the other side of the cord.

FIG. 38.—Decussation of pyramids. Scheme showing passage of various tracts from cord to medulla. (Testut.)



a. Pons. *b.* Medulla from the front. *c.* Decussation of pyramids. *d.* Spinal cord. 1. Direct pyramidal tract (red). 2. Crossed pyramidal tract (red). 3. Columns of Goll and Burdach (blue). 3'. Gracile and cuneate nuclei. 4. Antero-lateral basis bundle. 5. Pyramid. 6. Fillet. 7. Posterior longitudinal fasciculus. 9. Direct cerebellar tract (yellow).

The fibres of the pyramidal tracts terminate by arborising around cells of the posterior horn, the axons of which in turn arborise around motor cells in the anterior horn. By this arrangement an impulse passing down a pyramidal fibre will set in action not simply a single muscle but a co-ordinated group of muscles which customarily act together (Fig. 42).

Columns of Goll and of Burdach.—

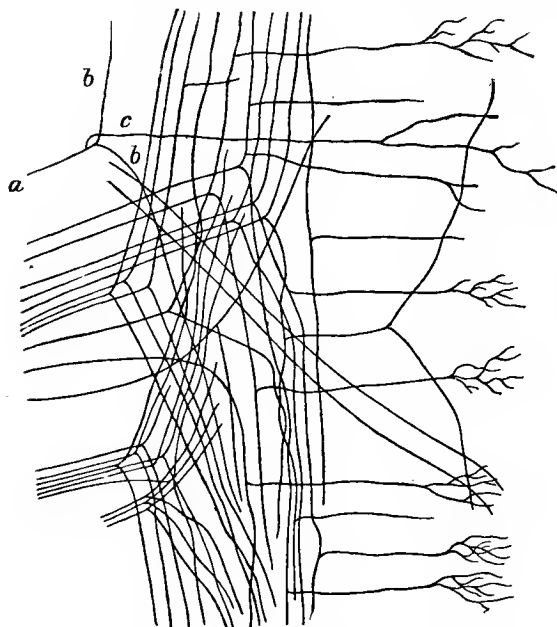
These comprise four great sensory tracts—two on either side of the posterior median septum—which convey impulses up towards the brain; the columns of Goll are the innermost and lie one on either side of the septum. They are made up mainly of the axons of the bipolar cells of the posterior root ganglia of the spinal nerves. The axon enters the cord close behind the apex of the posterior horn and gives off a large descending collateral branch which runs downwards, forming by its secondary branches arborisations around cells in all parts of the grey matter (Fig. 39). The axon itself passes upwards, close to the mesial aspect of the posterior horn, in the column of Burdach; as it ascends it inclines more and more towards the median septum, and, if it be from one of the lower nerves, enters the column of Goll and so proceeds to the medulla. It will be evident, there-

fore, that the separation of the columns of Goll and Burdach is mainly descriptive; in a section across the cord close to the medulla, axons from all the posterior roots will be found—those from the lowest (sacral and lumbar) nerves lying nearest the middle line, while those from the upper (cervical) are further out close to the mesial aspect of the posterior horn (Fig. 40).

Some of the fibres which enter the tract of Burdach do not run to the medulla

but pass off at intervals into the base of the posterior horn arborising round its cells. The most notable of this series are those which arborise around the cells of Clarke's column.

FIG. 39.—Dorsal roots entering cord and dividing into ascending and descending branches. (Van Gehuchten.)



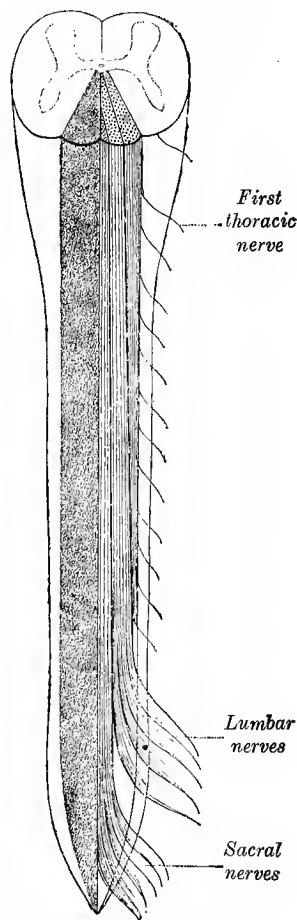
a. Stem-fibre. b, b. Ascending and descending limbs of bifurcation.
c. Collateral arising from stem-fibre.

Direct Cerebellar Tract.—The fibres of this tract arise from the cells of Clarke's column. They run upwards on the outer side of the crossed pyramidal tract into the medulla and thence to the cerebellum (Figs. 37 and 38).

Functions of the Spinal Cord.—The spinal cord subserves two functions: (1) it is a centre for reflex actions; (2) it is a great conducting path to and from the higher centres.

In discussing reflex actions (p. 16) it was pointed out that the reflex pathways in the higher animals are all of a complex type. Some of the main modification of the arcs, as seen in

FIG. 40.—Formation of the column of Goll. (Poirier.)

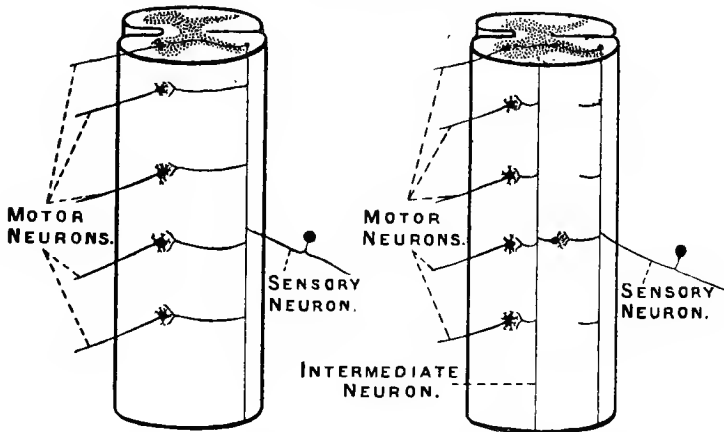


Spinal cord viewed from behind. To the left the column of Goll is shaded. To the right the drawing shows that the column of Goll is formed by the long fibres of the posterior roots, and that in this tract the sacral nerves lie next the mesial plane, the lumbar to their outer side, and the thoracic still more laterally.

the spinal cord, may now be indicated. For convenience they may be divided into: (a) those of the afferent portion of the arc; (b) those of the efferent portion of the arc.

(a) The entering axon of a sensory neuron sends a long branch downwards in the cord. Collaterals from this arborise round cells at the apex of, and in the substance of, the posterior horn. The axons of these in turn arborise round one or more motor cells of the anterior horn of the same or opposite side of the cord. The outstanding modification introduced thus is the interposition of an intermediate neuron between the motor and sensory neurons. Other modifications are (1) the linking up of the sensory neuron with several of these

FIG. 41.—Scheme showing modifications of the afferent arms of the reflex pathways in the spinal cord.



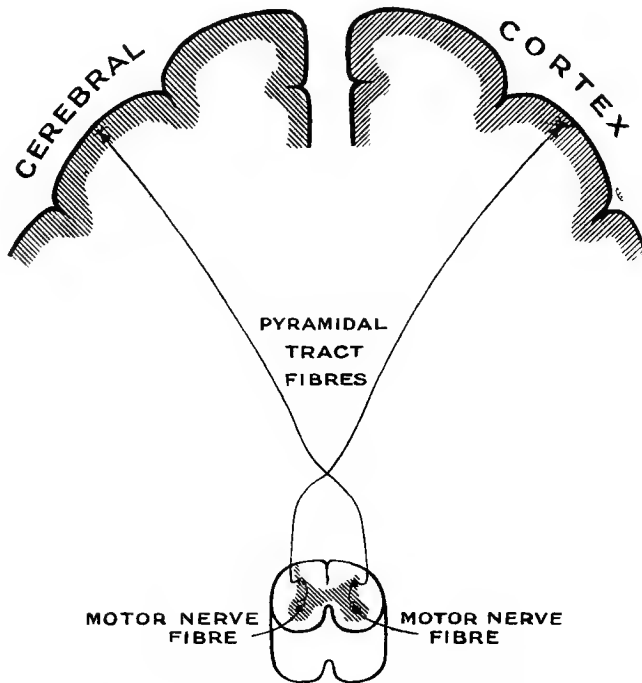
intermediates and (2) the communication of each intermediate with several motor neurons (Fig. 41).

These modifications are still more strikingly evident when the main stems of the entering sensory axons are traced. These run up in the columns of Goll and Burdach, towards the medulla where they arborise round cells in this part of the brain. From these in turn fibres arise, cross to the opposite side of the brain and pass on to the great ganglia at the base of the brain. A third set of fibres runs thence up to the surface of the cerebral hemispheres. All these fibres give off side branches, so that the communications they form are multitudinous.

(b) Some of the twigs of the sensory collaterals pass directly to arborise round the motor cells of the anterior horn (Fig. 41), and this represents the simplest type of reflex pathway found in the higher animals. In most, however, the intermediate neuron is interposed.

The long motor pathway presents the best example of modification of the efferent part of the arc. It begins in cells in the surface of the brain. The axons of these cells extend down as the fibres of the pyramidal tracts to cells in the posterior horn of the grey matter of the cord. From these, new fibres pass to the motor cells of the anterior horns whence the outgoing fibres to the muscles, etc., are derived (Fig. 42).

FIG. 42.—Scheme showing modification introduced into the efferent arm of the long reflex pathway.



From the physiological standpoint the chief modification in the reflex pathways is that the efferent portions of the arcs are not simply in communication with afferent fibres entering through the posterior spinal roots, but are also intimately connected with fibres from higher levels of the cord and from the brain. Quite apart from any influence of the will, the impulses from above exert an inhibitory effect on the spinal reflexes and this can be demonstrated in two ways. If certain regions of the brain be stimulated, reflex actions in the cord may be either greatly diminished or completely stopped; if, on the other hand the brain be cut away, the spinal reflexes become greatly exaggerated. By the exercise of will power, spinal reflexes, even such a vital one as the

movements of the respiratory muscles, may be partially controlled. A striking example of a similar nature, and one which shows also the close connection of the several regions of the central nervous system, occurs when by concentrating the attention on one reflex another may be completely suppressed, e.g. a man engaged in a strenuous contest may receive injuries which at the time pass completely unnoticed by him.

For the investigation of the reflex centres in the cord it is necessary therefore to completely interrupt its continuity with the brain. This destroys all sensation in the trunk and limbs, prevents any voluntary movements, and breaks the long reflex pathways which have their centres above the level of the cord. The long reflex pathways become more important with each increase in nervous organisation, so that in the lower vertebrates (fishes, frogs, etc.) the spinal cord is a much more independent structure than it is in man. These lower animals are therefore used largely for demonstrating spinal reflexes. In the higher animals after any severe operation on the cord the animal suffers from a considerable degree of shock which abolishes or obscures many of its reflex functions. If the animal can be kept alive until shock is recovered from, it will be found that the cord regains many of its powers and is capable of carrying out important complex reflex actions. Thus if the spinal cord of a dog be divided in the thoracic region, and the animal be kept alive, the reflexes controlling defæcation, micturition, parturition, etc., will ultimately prove effective.

Special Conducting Paths in the Cord.—So far the term sensory tract has been used to designate collectively all forms of sensation. Observations, however, have shown that the different forms of sensation travel by different paths along the cord. No dogmatic statements are possible regarding these, but it seems probable that the fibres conveying the sensations of touch, pain, and temperature are those of the short tracts in the antero-lateral basis bundles; the long tracts are mainly concerned in conveying the various muscular sensibilities. All of these will, however, be considered later.

CHAPTER V

THE HIND-BRAIN

THE hind-brain comprises the medulla oblongata or bulb, the pons Varolii, and the cerebellum. Within it, is a shallow diamond-shaped cavity—the fourth ventricle. The medulla and pons form the floor of this cavity; the cerebellum lies in the upper part of the roof, while the lower part of the roof is devoid of nervous material, and is composed merely of the lining membrane of the ventricle covered by the pia mater.

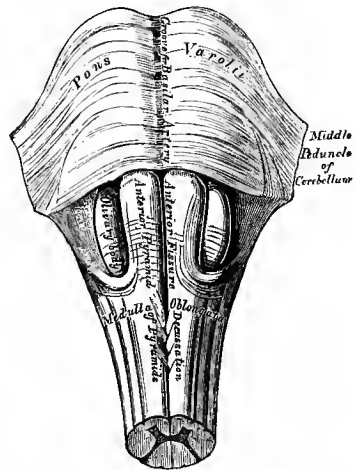
Medulla Oblongata and Pons Varolii.

External Appearances.—The medulla oblongata, about an inch in length, is directly continuous with the upper end of the spinal cord. In form it resembles a truncated cone with its base upwards and applied to the pons. The pons Varolii presents the appearance of a prominence composed of transverse strands which narrow towards either side and are continued into the cerebellum. A broad shallow median groove extends down its anterior surface (Fig. 43).

Along the anterior surface of the medulla the anterior median fissure runs from the spinal cord up to the margin of the pons. The posterior median fissure is continued for about halfway up the medulla; at this level the central canal, which has been gradually approaching the posterior surface, opens up by the divergence of the posterior columns, and becomes the cavity of the fourth ventricle (Fig. 44).

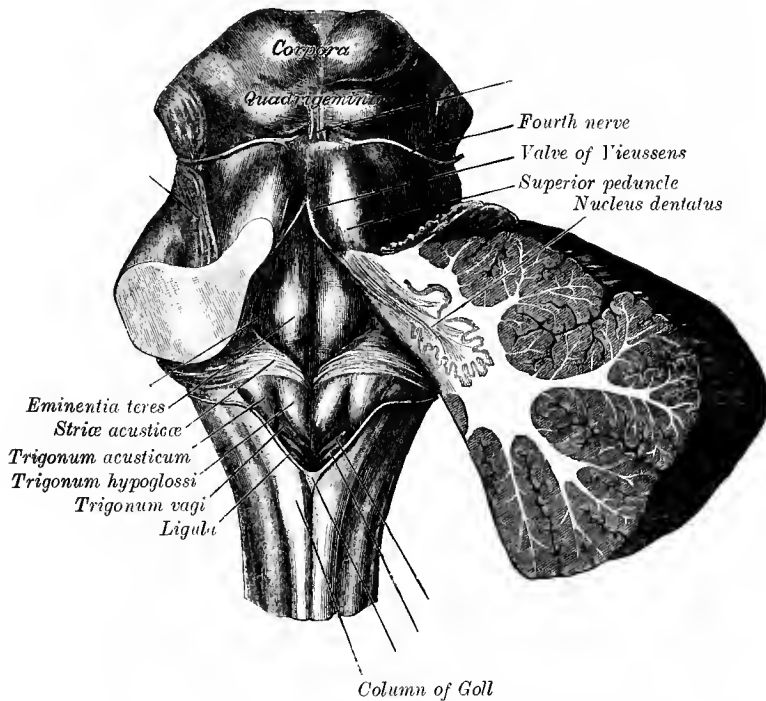
On either side of the anterior median fissure is a pear-shaped swelling—the pyramid—which contains in its upper part the undivided pyramidal tracts. When it is traced downwards towards the spinal cord the decussating portions of the tracts can be seen interlacing across the fissure. To the outer side of the pyramid is an oval swelling known as the olive; it contains some masses

FIG. 43.—Medulla oblongata and pons Varolii. Anterior surface.



of grey matter—the inferior olivary nuclei. On the posterior surface of the lower part of the medulla the continuations of the columns of Goll and of Burdach can be seen. They are rendered more evident here by the fact that in each there is a nucleus of grey matter giving rise to a distinct surface elevation. These elevations are known respectively as the gracile tubercle on the column of Goll, and the cuneate tubercle on the column of Burdach. When

FIG. 44.—Floor of fourth ventricle.



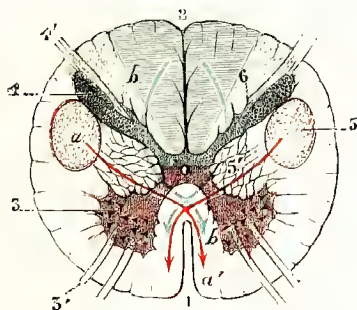
traced upwards the columns of opposite sides diverge widely from one another, and disappear from surface view. Their place is taken by a rope-like elevation—the restiform body—which superficially seems to be their continuation, but is not really so. The restiform body lies immediately behind the olive and passes upwards and outwards to the cerebellum. The rest of the posterior surface of the medulla, together with the posterior surface of the pons, form the floor of the fourth ventricle.

From the anterior and lateral surfaces of the pons and medulla the fifth to the twelfth cerebral nerves emerge as seen in Fig. 55.

Internal Structure.—The main feature of the internal structure of the medulla and pons is that the grey matter is no longer arranged in one continuous

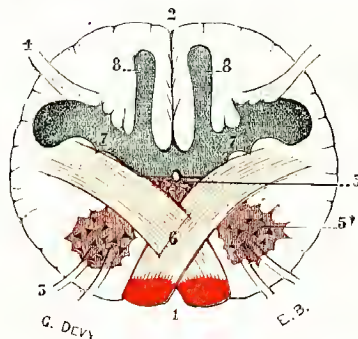
column round the central cavity as in the spinal cord, but is cut up into small independent portions or nuclei scattered amongst interlacing fibres. Some of these nuclei correspond to definite portions of the grey matter of the spinal cord, but a considerable number of new nuclei appear which are not apparently represented in the cord. The three great factors instrumental in breaking up the regular arrangement of the grey matter are : (1) The motor decussation ; (2) the sensory decussation ; (3) the expansion of the central canal into the fourth ventricle.

FIG. 45.—Section of the medulla through the lower part of the decussation of the pyramids. (Testut.)



1. Anterior median fissure. 2. Posterior median fissure. 3. Anterior horn (in red), with 3', anterior root. 4. Posterior horn (in blue), with 4', posterior roots. 5. Crossed pyramidal tract. 6. Posterior column. The red arrows, *a, a'*, indicate the course the crossed pyramidal tract takes at the level of the decussation of the pyramids; the blue arrows, *b, b'*, indicate the course which the sensory fibres take.

FIG. 46.—Section of the medulla at the level of the decussation of the pyramids. (Testut.)



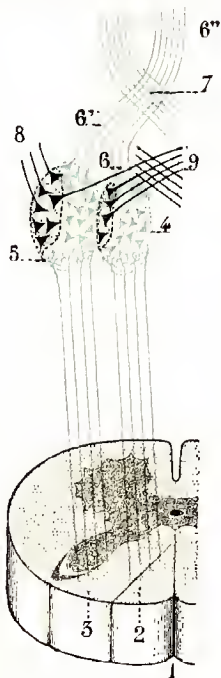
1. Anterior median fissure. 2. Posterior median fissure. 3. Motor roots. 4. Sensory roots. 5. Base of the anterior horn, from which the head (5') has been detached by the crossed pyramidal tract. 6. Decussation of the crossed pyramidal tracts. 7. Posterior horns (in blue). 8. Gracile nucleus.

(1) To facilitate the understanding of this region it is convenient to trace the pyramidal tracts upwards from the spinal cord, although it must be borne in mind that the impulses which they convey travel downwards.

Just beyond the spinal cord, at the region of the pyramidal or motor decussation, the crossed pyramidal tracts run forwards and inwards and cross the anterior median fissure to join the direct pyramidal tracts of the opposite sides. In their passage they cut through the anterior horns of grey matter, separating off completely the apices of these, but leaving the basal portions in the floor of the central canal (Figs. 45 and 46). The apex of the horn, thus pushed aside, forms a nucleus termed the nucleus ambiguus; the axons of its cells take part in the formation of several of the cerebral nerves, viz., part of the spinal accessory (xi), and the motor portions of the vagus (x) and glossopharyngeal (ix). Further forward in serial continuity with it are the nuclei of the motor portions of the facial (vii) and trifacial (v).

(2) With the posterior horn of the grey matter on either side two masses are connected. One, situated in the gracile tubercle on the column of Goll, is known as the nucleus gracilis; around its cells the fibres of the column of Goll terminate by arborisations. The other, in the cuneate tubercle on the column of Burdach, is termed the nucleus cuneatus; it forms a similar terminus

FIG. 47.—Superior terminations of the posterior tracts of the spinal cord. (Testut.)

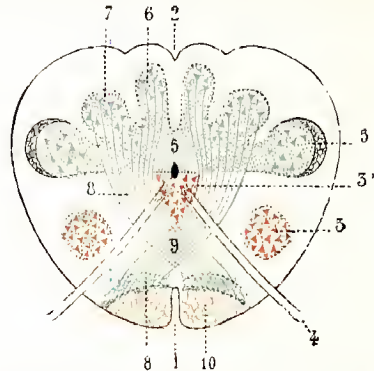


1. Posterior median fissure. 2. Column of Goll. 3. Column of Burdach. 4. Gracile nucleus. 5. Cuneate nucleus. 6, 6', 6'', Sensory fibres forming the fillet. 7. Sensory decussation. 8, 9. Cerebellar fibres.

the pyramid, and termed the fillet. By this, which is designated the sensory decussation, the apices of the posterior horns of grey matter are cut off and become the tubercles of Rolando; the basal portions of the horns remain in contact with the central canal (Fig. 48).

Fibres of the antero-lateral basis bundles of the spinal cord are continued up into the medulla, behind the fillets, as two strands (one on either side) known as the posterior longitudinal fasciculi. They retain their spinal characteristics, i.e. they consist of short fibres linking up the various grey nuclei.

FIG. 48.—Transverse section passing through the sensory decussation. (Schematic.) (Testut.)



1. Anterior median fissure. 2. Posterior median fissure. 3, 3'. Head and base of anterior horn (in red). 4. Hypoglossal nerve. 5, 5. Posterior horn (in blue). 6. Gracile nucleus. 7. Cuneate nucleus. 8, 8. Fillet, or sensory tract. 9. Sensory decussation. 10. Pyramidal tract.

for the fibres of the column of Burdach (Fig. 47). From the cells of these nuclei new fibres arise; some of them pass, either directly or after decussation, into the restiform body and thence to the cerebellum; the majority, however, run towards the middle line, where they decussate with those of the opposite side, and are then continued up as a flattened band situated immediately dorsal to

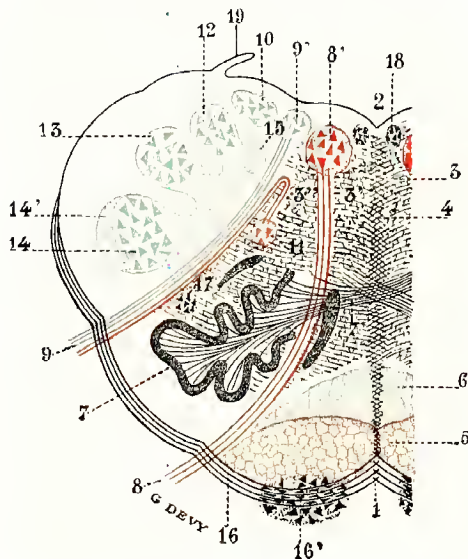
(3) When the central canal of the lower part of the medulla opens up into the fourth ventricle the continuations of the basal parts of the anterior horns come to the surface in the floor of the ventricle immediately adjacent to the middle line. From them the nuclei of the hypoglossal (xii) and abducent (vi) nerves are formed. The continuations of the basal parts of the posterior horns are displaced to the outer sides of these. They are resolved into the sensory nuclei of the vagus (x), glossopharyngeal (ix), facial (vii), and trifacial (v) nerves (Figs. 49 and 50).

The main additional grey nuclei which are present in the medulla and pons are: (1) the inferior olivary nuclei, the axons of some of the cells of which run to the cerebrum, others to the cerebellum; (2) the superior olives; (3) a group of small nuclei in the pons termed the nuclei pontis; (4) the accessory nuclei of the auditory nerves.

Cerebellum. — *External Appearances.*—The cerebellum consists of three lobes—one median, known as the vermis or worm, and two lateral, the cerebellar hemispheres. On the upper surface the vermis presents as a slight median elevation between the hemispheres; on the under surface it lies at the bottom of a deep groove and is partly hidden by the overlapping of the hemispheres.

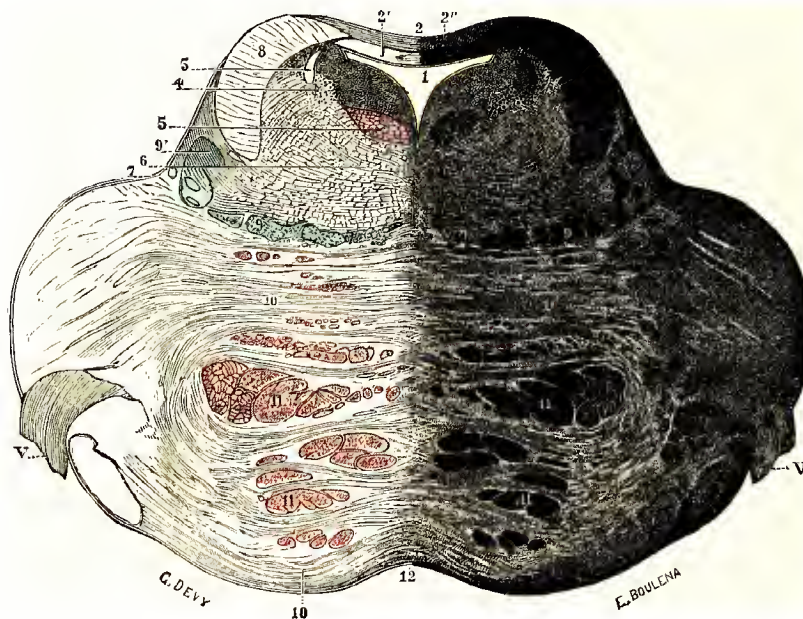
The surface of the cerebellum is incised by a series of slightly curved transverse fissures, practically parallel to one another and lying very close together (Fig. 51). Some of the fissures extend for a considerable distance into the cerebellar substance, and are used for descriptive purposes to divide the cerebellum into lobes which, however, are of no specific physiological importance. The cerebellum is connected with the rest of the brain by three roots or peduncles—superior, middle, and inferior—on either side. The superior peduncles run upwards towards the mid-brain, gradually converging towards one another as they ascend. They are connected to one another by a thin plate of nervous tissue—the valve of Vieussens—and disappear from surface view under

FIG. 49.—Transverse section of the medulla passing through the inferior olivary nucleus. (Testut.)



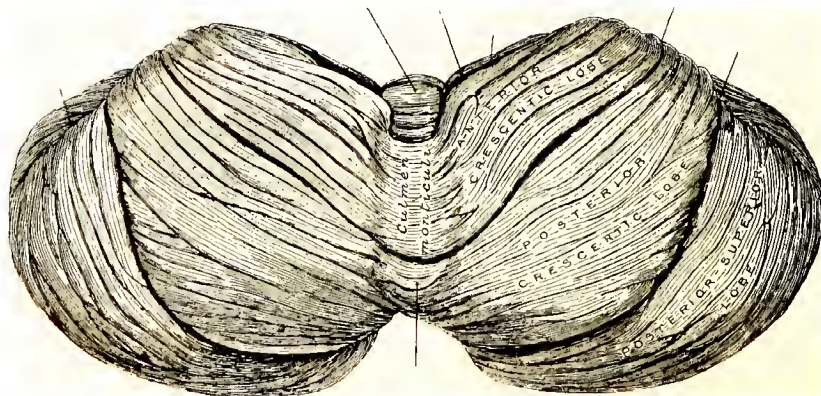
1. Anterior median fissure. 2. Fourth ventricle. 5. Pyramid. 6. Fillet. 7. Inferior olivary nucleus. 8. Hypoglossal nerve, with 8', its nucleus. 9. Vagus, with 9', its nucleus. 11. Nucleus ambiguus. 12. Gracile nucleus. 13. Cuneate nucleus. 14. Head of posterior horn.

FIG. 50.—Transverse section of the pons at its upper part. (Testut.)



1. Fourth ventricle. 2. Valve of Vieussens. 4. Nucleus of the trifacial nerve. 5. Posterior longitudinal fasciculus. 8. Section of superior cerebellar peduncle. 9. Mesial fillet. 9'. Lateral fillet. 11, 11. Pyramidal fibres. V. Trifacial nerve.

FIG. 51.—Upper surface of the cerebellum. (Schäfer.)



the inferior corpora quadrigemina. The middle peduncles are the great transverse strands which give form to the pons Varolii. The inferior peduncles are the continuations of the restiform bodies of the medulla (Fig. 52).

Internal Structure.— If the cerebellum be cut across in vertical antero-posterior sections the laminated or foliated appearance produced by the fissures of the surface is well demonstrated. Further it will be seen that the central part consists largely of white fibres, amongst which, however, are some independent masses of grey matter; the largest of these latter are known as the dentate nuclei (one in each hemisphere). The whole cerebellar surface is formed of grey matter which completely covers each individual lamina and lines all the fissures (Fig. 53).

FIG. 53.—Vertical antero-posterior section through right cerebellar hemisphere and right olivary body.

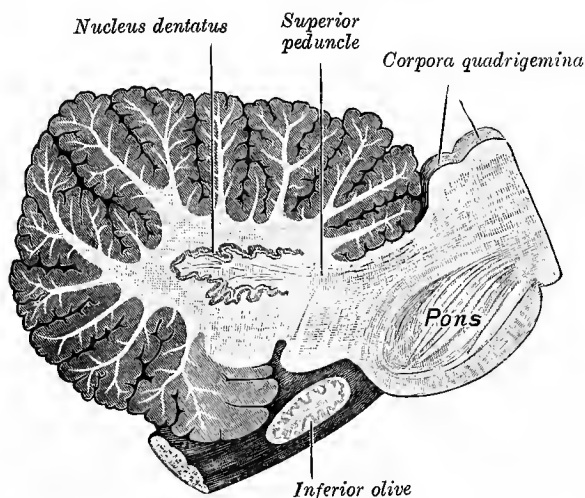
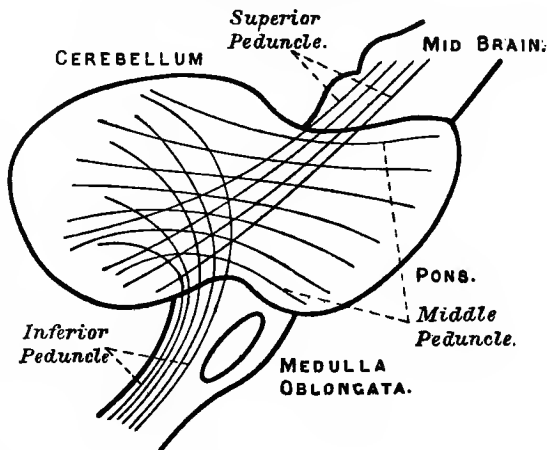


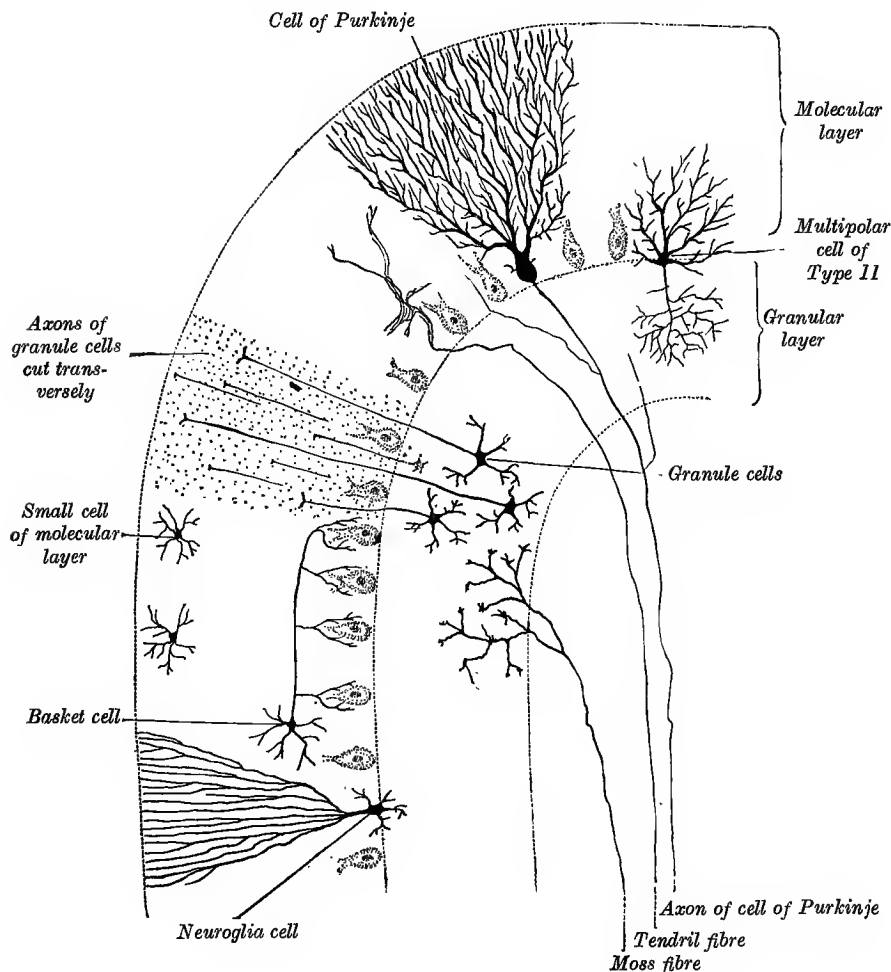
FIG. 52.—Scheme showing arrangement of the cerebellar peduncles.



In the grey matter of the cerebellum many of the already described fibres of the medulla terminate. Thus, entering by the inferior peduncle are: the direct cerebellar tract, fibres from the gracile and cuneate nuclei, and fibres from the inferior olivary nuclei. An important set of fibres entering by this route are those from the auditory nerve, which will be described later. Running in by the middle peduncle are fibres derived from the small nuclei pontis. The superior peduncle is

made up chiefly of fibres emerging from the dentate nucleus; it contains, however, some entering fibres from the spinal cord.

FIG. 54.—Transverse section of a cerebellar folium. (Diagrammatic, after Cajal and Kölliker.)



The grey matter of the cerebellar cortex contains cells of many forms. There is, however, one form which is peculiar to this region, viz. that of the cells of Purkinje. These cells have the shape of flasks flattened from side to side; from the neck of the flask numerous dendritic branches pass to the surface of the cerebellum; from the base of the flask a long axon passes into

the central white matter. The most readily defined of the other cells in the cortex are a series of small cells, the axon of each of which forms arborisations round several cells of Purkinje (Fig. 54).

Fourth Ventricle.—The floor of the fourth ventricle is of such great physiological importance that a further description of it is necessary. In outline the floor is diamond- or lozenge-shaped. The lower boundaries are formed by the columns of Goll and the restiform bodies ; the inferior angle, at the point of divergence of the columns of Goll, is termed the *calamus scriptorius*. The upper boundaries are formed by the superior peduncles of the cerebellum. The floor is divided by a median longitudinal furrow or groove, and each half is subdivided into an upper and a lower part by some superficial transverse fibres connected with the auditory nerve, and known as the *striæ acusticæ* (Fig. 44).

Immediately within each lateral angle is a rounded elevated surface—the *tuberculum acusticum*—underneath which are certain nuclei of the auditory nerve. Lying alongside the median groove on either side is a narrow rounded elevation, which extends from the upper to the lower angle. Below the *striæ acusticæ* it is known as the *trigonum hypoglossi* and is caused by the nucleus of the hypoglossal (xii) nerve. Above the *striæ acusticæ* it is more prominent and presents a distinct swelling in the middle ; it is here termed the *fasciculus teres*, and the swelling (*eminentia teres*) overlies the nucleus of the abducent (vi) nerve. Between the *trigonum hypoglossi* and the *tuberculum acusticum* is a triangular depression—the *trigonum vagi*—beneath which are the sensory nuclei of the vagus (x) and glossopharyngeal (ix) nerves. The area between the *fasciculus teres* and the *tuberculum acusticum* is situated over the chief nuclei of the trifacial (v) nerve.

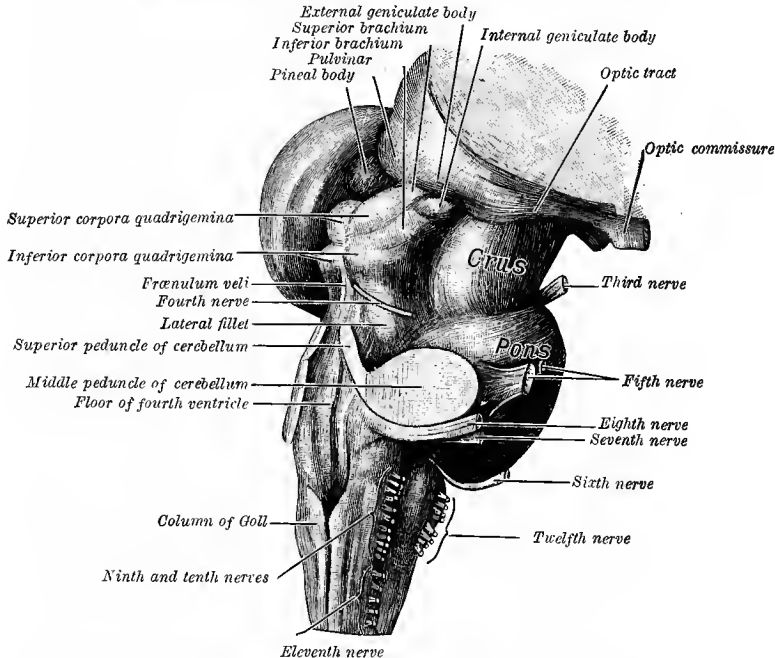
A reference to the general functions of the cerebral nerves (p. 27), which originate or terminate in this region, will show that it is an exceedingly important reflex centre. Impulses are constantly arriving in it from all the organs of nutrition and from the head and neck, while other impulses are passing out to the motor apparatus of the organs of nutrition, to the muscles of mastication and expression, and to the muscles of the tongue and neck.

CHAPTER VI

THE MID-BRAIN

THE mid-brain is a short stem which serves mainly as a conducting path between the fore- and hind-brains. Its upper or dorsal part consists of the corpora quadrigemina; the remainder forms the crura cerebri or peduncles of the brain.

FIG. 55.—Hind- and mid-brains; viewed from the side and back.



The original cavity of the mid-brain vesicle is represented by a fine canal, the iter or aqueduct of Sylvius, which is continued behind into the fourth ventricle, and opens in front into the third ventricle.

External Appearances.—On the upper surface are four small rounded eminences—the corpora quadrigemina—separated from one another by a crucial

groove. They are arranged in pairs : two superior or anterior associated with the sense of sight, and two inferior or posterior associated with the sense of hearing. Passing outwards from the side of each is a rounded strand of fibres, the brachium. Each superior brachium terminates partly in a small elevation—the external geniculate body—and is partly continuous with the optic tract. Each inferior brachium runs into a little globular swelling—the internal geniculate body (Fig. 55).

The inferior and lateral surfaces of the mid-brain are composed of the crura cerebri. Each crus is made up of two parts : an upper portion designated the tegmentum, and a lower, the crusta. A groove on the surface—the lateral sulcus—indicates the division. The tecta are continuous from side to side of the mid-brain, but the crustæ of opposite sides are separated from one another by a deep interpeduncular groove. From slight furrows or sulci (oculomotor sulci) on the sides of this groove the third cerebral nerves emerge. Where the crura adjoin the pons they lie close to one another, but as they pass forwards they diverge, leaving a triangular interpeduncular space.

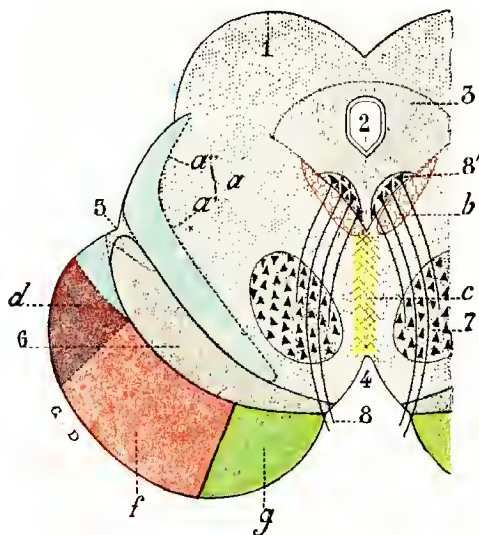
Internal Structure.—In a transverse section across the mid-brain the aqueduct of Sylvius can be seen near the superior surface (Fig. 56).

Grey Matter.—The important masses of grey matter of this region may be arranged in four groups : (1) the grey matter surrounding the aqueduct of Sylvius ; (2) the grey nuclei of the quadrigeminal bodies ; (3) the substantia nigra ; (4) the red nucleus.

(1) In the grey matter of the floor of the aqueduct of Sylvius the nuclei of the trochlear (iv), of the oculomotor (iii), and of a portion of the trigeminal (v) nerves are located.

(2) Around the cells of the inferior corpora quadrigemina, terminate many of the fibres of the lateral fillet, a band of fibres derived from certain nuclei of the auditory nerve in the medulla and pons. From the cells of the inferior corpora

FIG. 56.—Schematic transverse section through mid-brain. (Testut.)



1. Corpora quadrigemina. 2. Aqueduct of Sylvius. 3. Central grey matter of aqueduct. 4. Interpeduncular space. 5. Sulcus lateralis. 6. Substantia nigra. 7. Red nucleus of tegmentum. 8. Third nerve, with 8', its nucleus of origin. a. Fillet (blue), with a', the mesial fillet, and a'', the lateral fillet. b. Posterior longitudinal fasciculus. c. Descending fibres (red). d. Pyramidal fibres. e. Geniculate fibres.

quadrigemina fibres pass out by the inferior brachia into the tementa and run up to the fore-brain.

The fibres which enter the superior quadrigeminal body are derived from nerve cells of the retina ; they run in the superior brachium. Many of the emerging fibres pass out through the superior brachium to the fore-brain ; others, after decussating, are continued down through the pons and medulla to the spinal cord.

(3) The substantia nigra is a deeply pigmented mass of grey matter which extends across the crus from the lateral sulcus to the oculomotor sulcus, and separates the tegmentum from the crura.

(4) The red nucleus lies within the tegmentum. In it the fibres of the superior cerebellar peduncle terminate after decussation. A few of the fibres originating from the cells of the red nucleus pass up to the fore-brain, but the majority decussate and run down to the spinal cord.

White Matter.—The continuations of the important tracts already noticed in the medulla and pons can all be traced in the mid-brain. The crustæ consist practically entirely of motor fibres which originate in the cortex of the fore-brain. In the tegmentum the fillet lies above the substantia nigra : the outer portion of it—the lateral fillet—enters the inferior quadrigeminal body ; the remainder, named the mesial fillet, runs on to the fore-brain. The posterior longitudinal fasciculus is situated above the fillet and just below the grey matter of the aqueduct of Sylvius. From and to it pass fibres connecting the various nuclei in its vicinity.

CHAPTER VII

THE FORE-BRAIN

THE cerebral hemispheres grow to such a size in man that, with the exception of a few structures on the under surface, they are the only portions of the fore-brain visible on the exterior of the undissected brain. The structures referred to are (a) the olfactory tracts and bulbs, and (b) part of the floor of the third ventricle (the cavity within the back part of the fore-brain). From before backwards the latter presents : (1) the optic tracts coming downwards and forwards, one on either side ; they meet and partially decussate in the middle line, forming the optic commissure or chiasma and from this the two optic nerves (right and left) proceed to the eyeballs ; (2) the tuber cinereum, a small conical swelling from the apex of which extends a short stalk—the infundibulum—leading down to the pituitary body ; (3) the corpora mamillaria, two little spherical bodies lying side by side ; (4) the posterior perforated spot, a sieve-like area through which numerous small bloodvessels pass (Fig. 29).

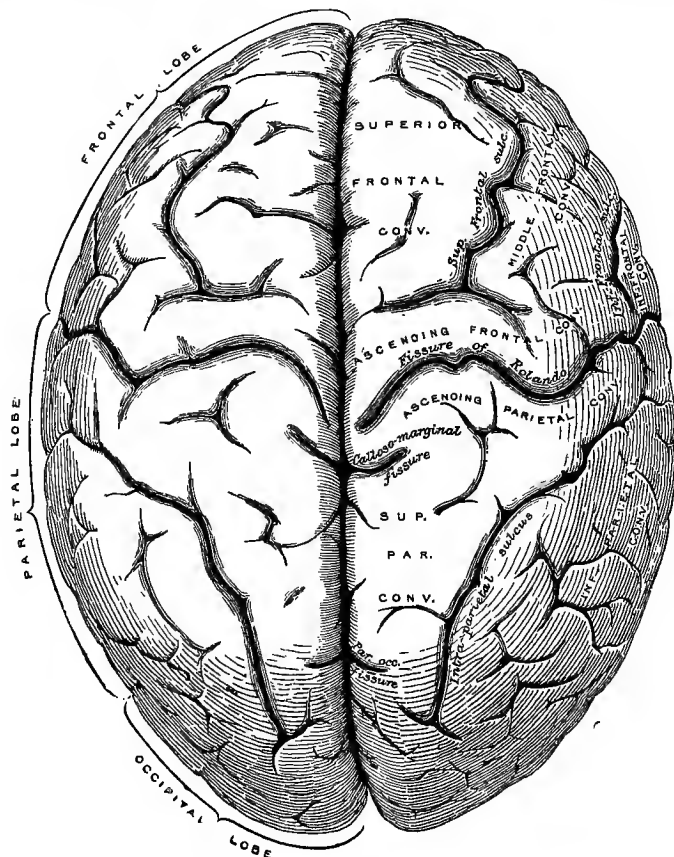
Cerebral Hemispheres.—*External Configuration.*—When viewed together the cerebral hemispheres have somewhat the appearance of the upper half of a sphere, but the antero-posterior diameter is greater than the transverse (Fig. 57). They present a large convex outer surface, which is adapted to the shape of the vault and sides of the skull, and a very irregularly flattened inferior surface. The greater part of the inferior surface is moulded on the irregularities of the bones forming the base of the skull, but its back part rests on a shelf of dura mater which intervenes between it and the cerebellum.

The hemispheres are separated from one another in the middle line by a deep cleft known as the great longitudinal fissure. The separation is complete in front and behind but only extends for about half the depth in the middle, the two hemispheres being joined to one another below this level by a large band of transverse fibres—the corpus callosum. Each hemisphere presents, therefore, three surfaces—outer, mesial, and inferior. The extreme anterior end of the hemisphere is the frontal pole, the posterior end is the occipital pole, while on the side the temporal pole projects forwards as the anterior extremity of a subdivision of the hemisphere termed the temporal lobe.

The surfaces of the hemispheres are marked by series of convolutions or gyri, separated by fissures or sulci of variable depths. The surface area is thus greatly increased without a corresponding increase of the bulk of the hemispheres.

The arrangement of the convolutions and fissures, which may be referred to as the brain pattern, bears no direct relationship to the location of the different functions of the cerebral hemispheres; it varies very greatly in different animals, and its intricacy is no measure of the degree of nervous organisation

FIG. 57.—Convulsions and sulci on the upper surface of the cerebral hemispheres.



of the animal. The brain pattern of man, however, is very intricate, and, further, it varies, within limits, in different individuals; there is a certain fairly definite ground plan common to all, but the individual embellishments are as varied as are the features in individual faces.

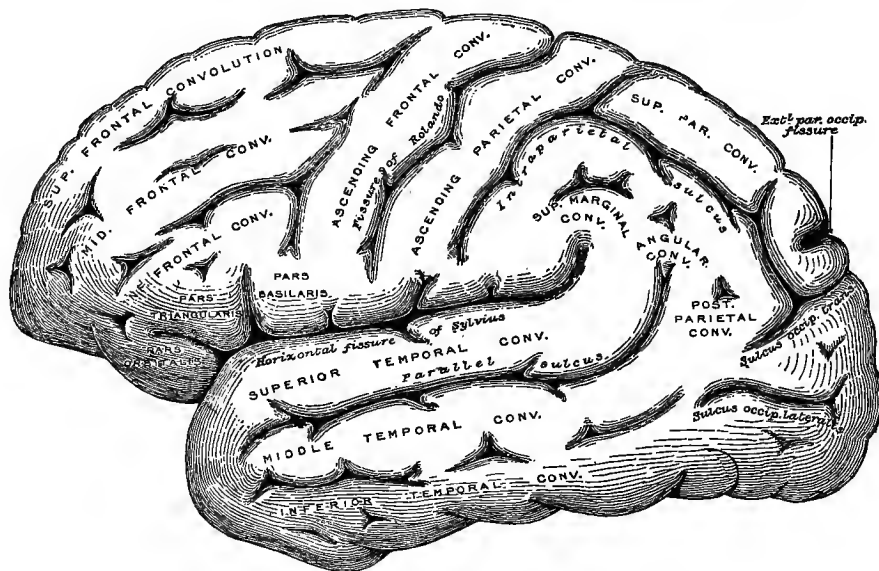
The more constant fissures are utilised in the description of the functional areas on the hemispheres, and may therefore be briefly indicated.

Outer Surface.—The surface is divided, for convenience of reference, into

lobes ; these have no physiological significance. The fissures which demarcate them are termed interlobar ; they are, the fissure of Sylvius, the fissure of Rolando, the external parieto-occipital fissure, and the circular sulcus of Reil (Fig. 58).

FISSURE OF SYLVIIUS.—The fissure of Sylvius is a deep cleft which lies chiefly on the outer surface of the hemisphere. It begins on the under surface near the optic chiasma by a short stem which turns round the margin and divides into three limbs. Two are short—one (anterior) horizontal, the other

FIG. 58.—Convolution and sulci on the external surface of the cerebral hemisphere.



(ascending) vertical ; the third, about three inches in length, extends almost horizontally backwards and terminates in an upturned end. When the lips of the various parts of the Sylvian fissure are forced apart a sunken portion of the surface, termed the island of Reil, is exposed.

FISSURE OF ROLANDO.—The fissure of Rolando, or central fissure, notches the upper margin of the hemisphere about half an inch behind its middle. From this point it runs downwards and forwards on the outer surface, and terminates just above the posterior limb and behind the ascending limb of the Sylvian fissure.

EXTERNAL PARIETO-OCCIPITAL FISSURE.—The main portion of the parieto-occipital fissure is on the mesial surface of the hemisphere, but a small portion about half an inch in length, the external parieto-occipital fissure, extends on to the outer surface two inches in front of the occipital pole.

CIRCULAR SULCUS OF REIL.—This surrounds the island of Reil and marks it off from the rest of the outer surface of the hemisphere.

For mapping out the lobes on the outer surface of the hemisphere a line is taken from the external parieto-occipital fissure to a small notch on the inferior margin ; the posterior limb of the fissure of Sylvius is prolonged back to meet this line ; the fissure of Rolando is continued down to meet the fissure of Sylvius. Five lobes are thus demarcated : (1) the frontal lobe in front of the Rolandic fissure ; (2) the parietal lobe between the Rolandic fissure and the external parieto-occipital fissure ; (3) the occipital lobe behind the external parieto-occipital fissure ; (4) the temporal lobe below the posterior limb of the Sylvian fissure ; (5) the island of Reil.

The frontal, parietal, occipital, and temporal lobes are all described as continuous on to the mesial surface of the hemisphere, but no practical use is made of the description, so it may be neglected.

FRONTAL LOBE.—There are three fissures dividing this area into four convolutions. One, the precentral, lies parallel to the fissure of Rolando ; the convolution between these two fissures is termed the precentral or ascending frontal. The other two fissures, known respectively as the superior and inferior frontal run at right angles to the precentral. They intervene between the superior, middle, and inferior frontal convolutions. The posterior part of the inferior frontal convolution of the left side has a special interest ; it is known as Broca's convolution—after Broca, who described it as the centre for articulate speech.

PARIETAL LOBE.—Parallel to and behind the Rolandic fissure is the postcentral fissure demarcating the postcentral or ascending parietal convolution. From near the middle of this fissure a second fissure extends backwards at right angles, the combined fissures forming a $\perp$ -shaped fissure termed the intraparietal. The horizontal limb separates the superior from the inferior parietal convolution. In the latter are the upturned ends of the Sylvian fissure and the first temporal fissure ; the areas around these ends are known respectively as the supra-marginal gyrus and the angular gyrus.

OCCIPITAL LOBE.—Two fissures cross the surface of this lobe. The upper, placed a short distance behind the external parieto-occipital and usually continuous with the horizontal limb of the intraparietal fissure, is termed the transverse occipital fissure. The other—the lateral occipital fissure—runs horizontally across the lobe and divides it into superior and inferior occipital convolutions.

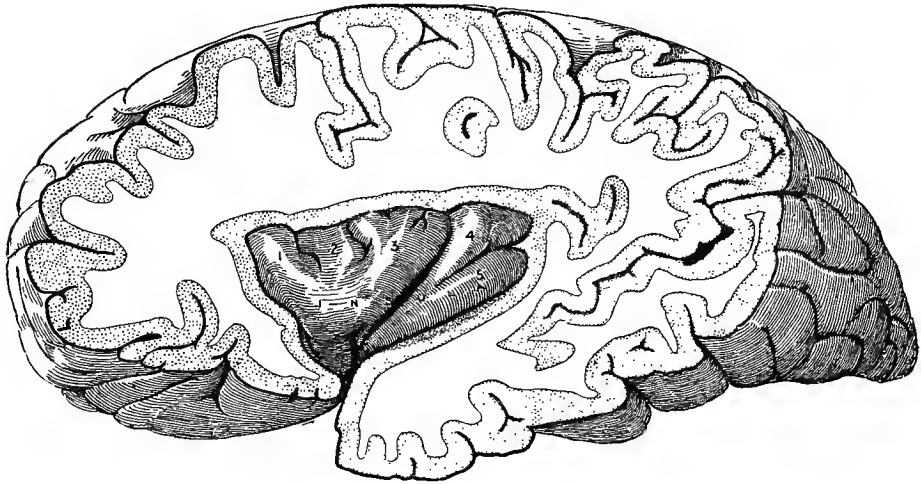
TEMPORAL LOBE.—This is traversed by two fissures parallel to one another and to the posterior limb of the Sylvian fissure ; they separate off the superior, middle, and inferior temporal convolutions.

ISLAND OF REIL.—The island of Reil is a submerged somewhat triangular portion of brain surface which is completely concealed from view by the overlapping of the adjacent lobes (Fig. 59). The covering portions are separated

from one another by the limbs of the fissure of Sylvius into a series of opercula ; they are : (1) the orbital operculum below the anterior limb of the Sylvian fissure ; (2) the frontal, between the anterior and ascending limbs ; (3) the fronto-parietal, between the ascending and posterior limbs ; and (4) the temporal, below the posterior limb.

Mesial Surface.—The mesial surface of the hemisphere cannot be fully exposed until the hemispheres have been separated from one another, and from the rest of the brain. The most prominent landmark on it is the cut surface of the corpus callosum which is shaped like an arch with its convexity upwards ;

FIG. 59.—The island of Reil. Left side. The overlapping parts of the hemisphere have been removed.



the anterior end of the arch is curved on itself to form the genu or knee which is prolonged into a thin pointed extremity, the rostrum ; the posterior end is sharply folded on itself, and presents a thickened pad, the splenium (Fig. 26).

The chief fissures on the mesial surface are the calloso-marginal, internal parieto-occipital, calcarine, collateral, and dentate (Fig. 60).

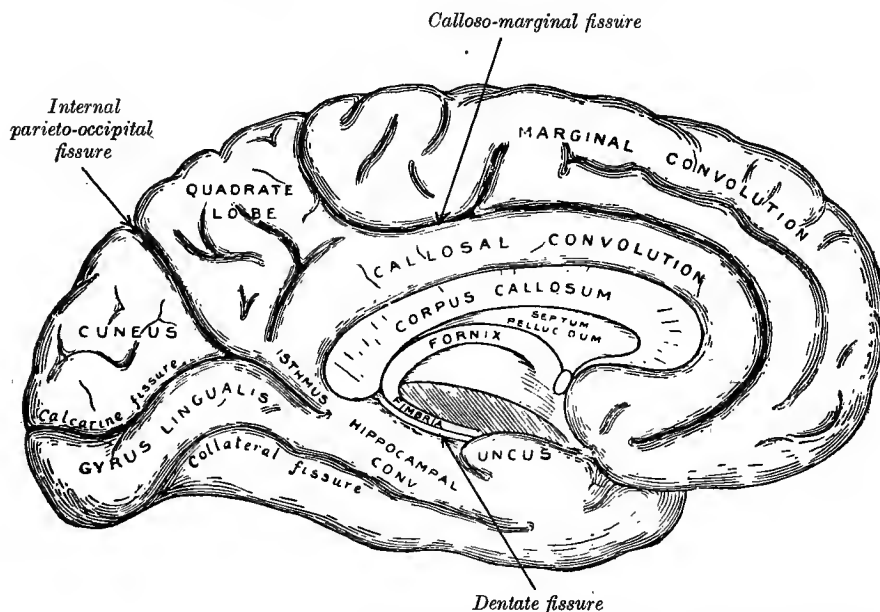
The CALLOSO-MARGINAL FISSURE lies practically parallel to the anterior two-thirds of the corpus callosum. It begins below the rostrum, curves round in front of the genu, and extends backwards to end by turning up to the superior margin just behind the fissure of Rolando. Between it and the corpus callosum is the callosal convolution ; above and in front of it is the marginal convolution.

The INTERNAL PARIETO-OCCIPITAL FISSURE is continuous with the external parieto-occipital of the outer surface. It runs downwards and forwards to

join the calcarine fissure. Between it and the upturned end of the callosomarginal fissure is an area termed the quadrate lobe or precuneus.

The CALCARINE FISSURE begins immediately above the occipital pole, and extends almost horizontally forwards to just behind the splenium. It is joined near its anterior third by the internal parieto-occipital fissure, and the two fissures mark off a triangular area known as the cuneus. Between the anterior portion of the calcarine fissure and the corpus callosum is a narrow convolution, the isthmus.

FIG. 60.—Mesial surface of left cerebral hemisphere.



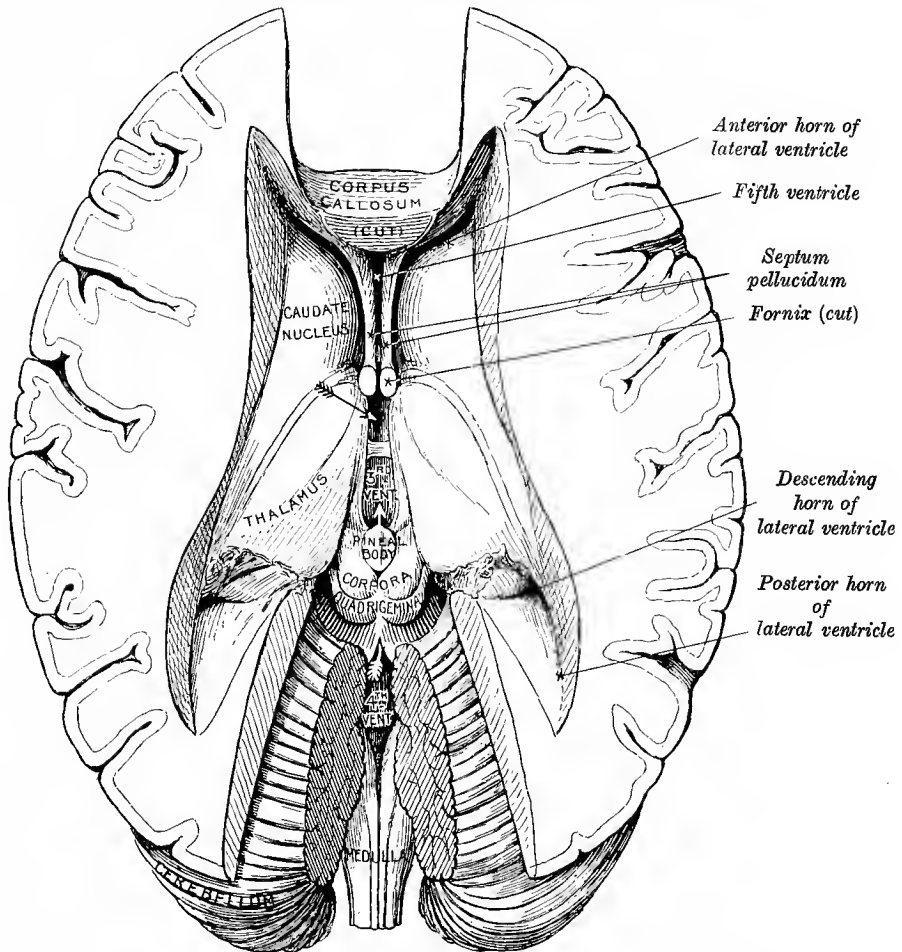
The COLLATERAL FISSURE reaches from the under surface of the occipital lobe towards the temporal pole. The lingual convolution separates its posterior part from the calcarine fissure.

The DENTATE FISSURE extends forwards from the splenium of the corpus callosum to a hooked surface prominence called the uncus. Between the dentate fissure and the collateral fissure is the hippocampal convolution which is continued forwards into the uncus and is in continuity behind with the isthmus. The callosal convolution, the isthmus, and the hippocampal convolution form one continuous arch, which is designated the limbic lobe.

Inferior Surface.—The front part of the inferior surface rests over the orbit (the bony capsule containing the eyeball) and is hence termed the orbital surface. It presents, close to the middle line, an antero-posterior fissure—

olfactory sulcus—in which lies the olfactory tract. The rest of the orbital surface is divided by an H-shaped fissure. Further back, on the inferior surface,

FIG. 61.—Dissection showing the ventricles of the brain.



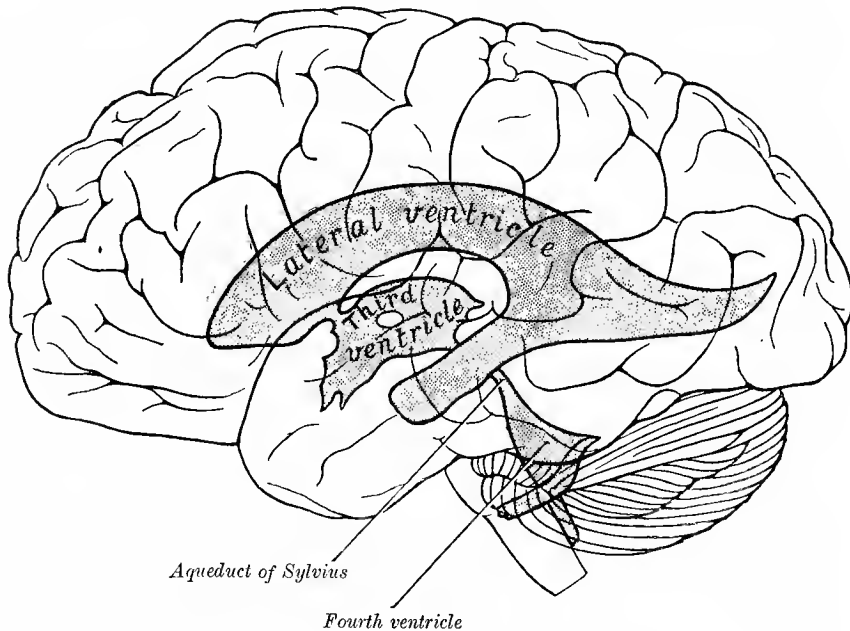
The upper arrow points to the foramen of Monro ; the lower arrow is in the aqueduct of Sylvius.

a long interrupted fissure—the occipito-temporal—extends between the occipital and temporal poles.

Internal Structure.—The internal structure of the fore-brain is so extremely complex that it is only possible to indicate in broad outline its main masses of grey matter, and its principal fibre systems.

Within the fore-brain there are three cavities or ventricles (Figs. 61 and 62). In the hinder portion is the third ventricle, a vertical median slit, which communicates behind with the aqueduct of Sylvius and through this with the fourth ventricle and the central canal of the spinal cord. In each of the cerebral hemispheres there is a cavity known as the lateral ventricle; it is prolonged into three diverticula or horns—*anterior, posterior, and lateral or descending, respectively*—so that the whole cavity is of a *triradiate form*. The two lateral

FIG. 62.—Scheme showing relations of the ventricles to the surface of the brain.



ventricles are separated from one another in the middle line by a partition called the *septum pellucidum*; behind this, they communicate with one another and with the third ventricle through the Y-shaped *foramen of Monro*. The *septum pellucidum* is really a double lamina and the cleft separating the two layers is designated the *fifth ventricle*; this space has no communication with any of the other ventricles.

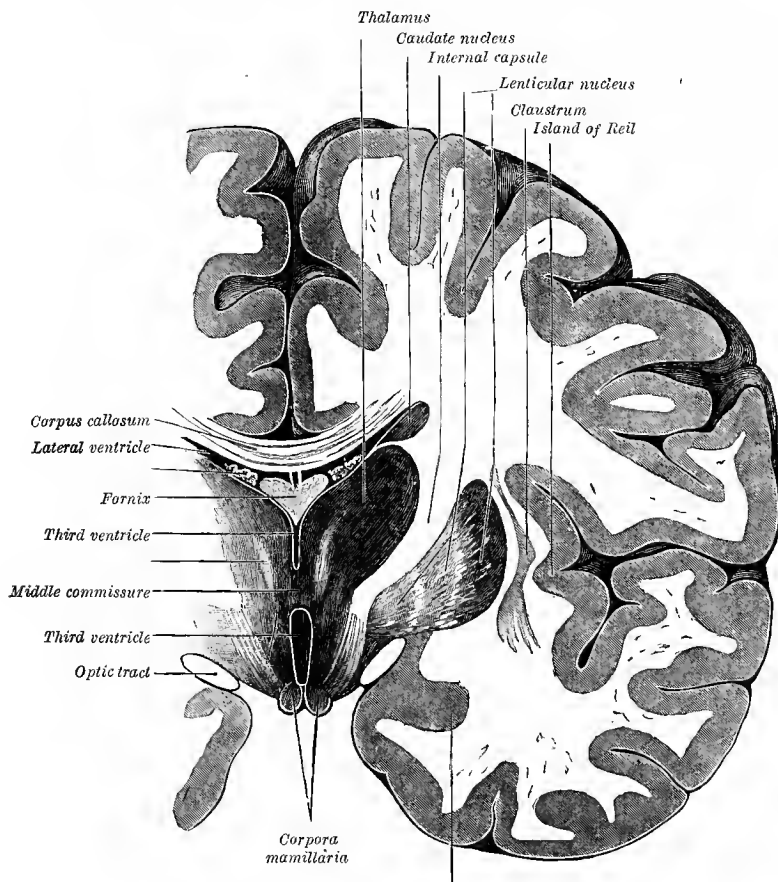
Grey Matter.—The chief grey matter of the fore-brain comprises: (1) the ganglia at the base; (2) the surface grey matter or cortex.

(1) The basal ganglia, two on either side, are the *thalamus* and the *corpus striatum*.

Thalamus.—The thalamus is a large ovoid mass which occupies the greater

part of the side wall of the third ventricle. Anteriorly its narrower extremity projects into the floor of the lateral ventricle (Fig. 61), while posteriorly its broader end overhangs the superior quadrigeminal body. On the posterior end

FIG. 63.—Vertical transverse section of brain through middle commissure.

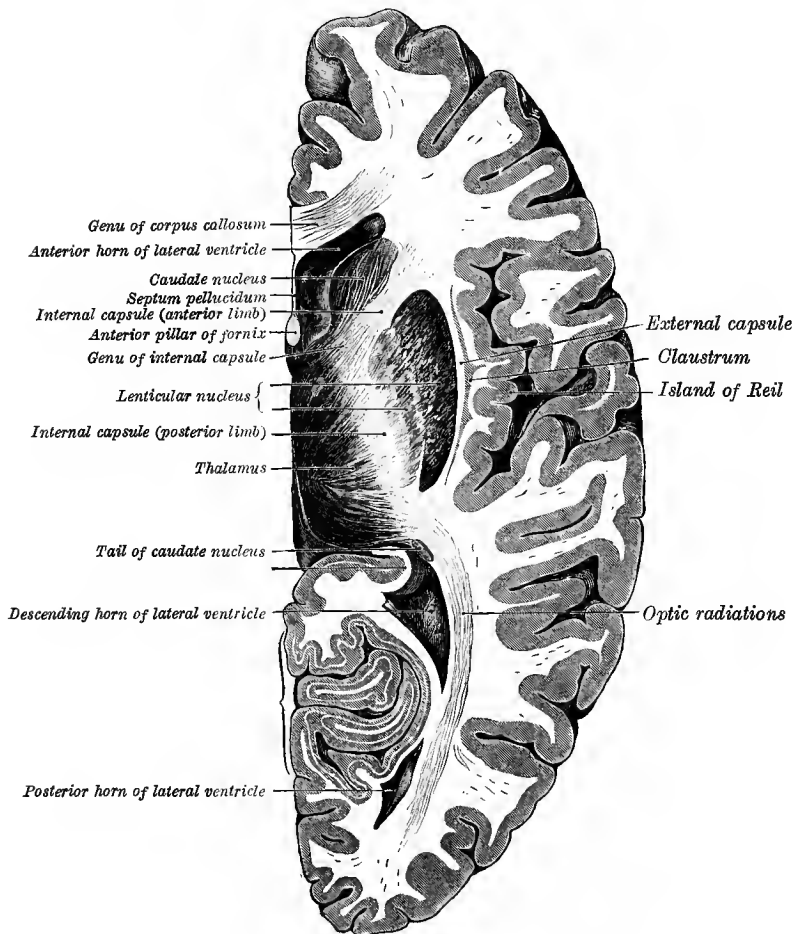


are three well-marked swellings; the internal is termed the pulvinar, the external is the external geniculate body, and the intermediate (posterior) is the internal geniculate body (Fig. 55). The two thalami are joined to one another across the middle line by a band of grey matter—the middle commissure (Fig. 63).

The thalamus is a great terminal nucleus for the sensory fibres ascending from the spinal cord and the hinder parts of the brain. Round its cells most of the fibres of the mesial fillet end by arborisation. It receives also fibres

from cells of the cerebral cortex. Its chief emerging fibres are arranged in four great groups or stalks : (a) anterior, to the frontal lobe ; (b) posterior, to the

FIG. 64.—Horizontal section of right cerebral hemisphere.



occipital lobe ; (c) inferior, to the island of Reil and temporal lobe ; (d) outer, to the parietal lobe. Many fibres also pass from and to the corpus striatum.

Corpus Striatum.—The corpus striatum owes its name to the striated appearance caused by the intermingling of numerous white fibres with the grey matter. It consists of two large nuclei which are completely separated from one another in the greater part of their extent, but are joined together

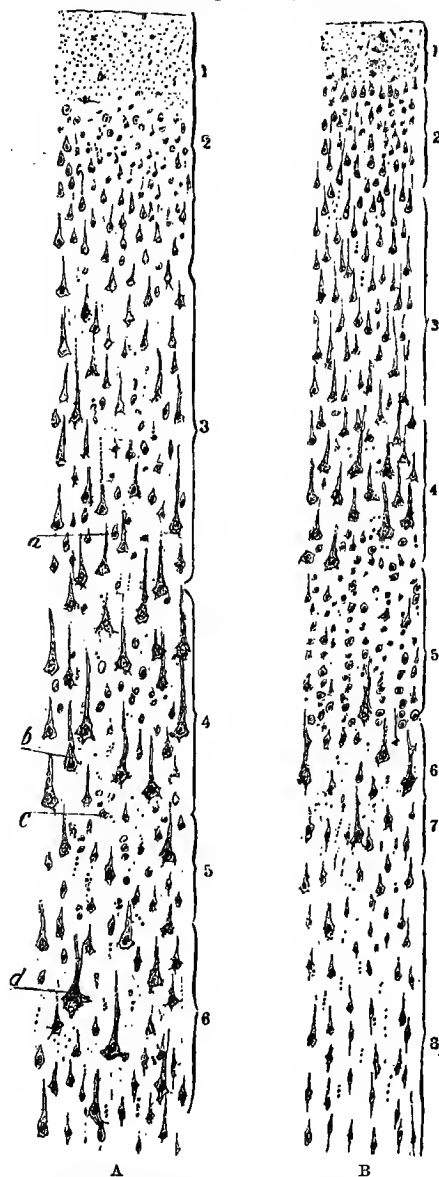
below at their anterior ends. The inner of the two nuclei is in contact with the anterior extremity of the thalamus and projects into the cavity of the lateral ventricle (Fig. 61); it is called the caudate nucleus. The outer nucleus is embedded in the white matter of the hemisphere and is termed the lenticular nucleus (Fig. 64).

In horizontal sections the lenticular nucleus is somewhat like a biconvex lens in shape; its internal surface is very sharply convex, the outer much less so. A flattened band of white fibres—the internal capsule—separates the internal surface from the caudate nucleus in front and from the thalamus behind. This band is sharply curved, like the surface of the lenticular nucleus with which it is in contact; the bend is known as the genu of the internal capsule, and the other portions are termed respectively the anterior and posterior limbs. In the white matter between the lenticular nucleus and the island of Reil is a thin vertical plate of grey matter—the claustrum.

The cells of the corpus striatum are principally of the multipolar type. They are connected by fibres to the thalamus and to the posterior parts of the brain. A striking fact is that very few fibres pass between the cerebral cortex and the corpus striatum.

(2) The entire surface or cortex of the cerebral hemispheres is composed of grey matter which covers all the convolutions and fissures. In different regions this cortical substance presents variations

FIG. 65.—Sections of cerebral cortex from two different regions. (Cajal.)



A. From precentral convolution (motor cortex). *a*, *c*, small cells amongst the pyramidal cells. *b*, A large pyramidal cell. *d*, A giant cell.
B. From postcentral convolution (sensory cortex).
The numbers at the sides of the sections bear no relation to the numbers in the text.

related to its functions (Fig. 65). These will be indicated later, but meantime some of its more constant elements may be enumerated. Five layers can be recognised. (1) A superficial layer of fibres (outer fibre lamina); (2) a layer of pyramidal cells (outer cell lamina); (3) a layer of small granular cells (middle cell lamina); (4) an inner layer of nerve fibres (inner fibre lamina); (5) a layer of polymorphic cells (inner cell lamina).

White Matter.—The white matter of the fore-brain occupies the region below and to the outer side of the thalamus (subthalamic region) and forms also the internal substance of the cerebral hemispheres. It consists of a close network of medullated fibres which may be grouped into three systems: (1) projection fibres, connecting the cortex with the rest of the brain and with the spinal cord. The chief descending projection fibres are those to the nuclei of the motor cerebral nerves and to the motor cells in the spinal cord; they rise from the pyramidal cells of the cortex, pass down in a series of converging strands—corona radiata—and then run through the genu and adjacent parts of the internal capsule. The ascending fibres run up through the extreme ends of the internal capsule; they are mainly derived from the thalamus, but amongst them are fibres of the mesial fillet and superior cerebellar peduncle which have escaped interruption; (2) commissural fibres between the two hemispheres. The largest strand of these is the corpus callosum; minor bands are the anterior commissure and the fornix; (3) association fibres—these fibres link up different portions of the same hemisphere, either adjacent convolutions (short association fibres) or distant portions (long association fibres).

CHAPTER VIII

THE CHIEF FIBRE SYSTEMS OF THE CEREBRO-SPINAL AXIS

IN the preceding chapters the principal tracts of nerve fibres have been studied in the separate portions of the brain and spinal cord. The results of these observations may now be combined and the various tract systems traced in their entirety.

As already indicated the fibres of the cerebro-spinal axis may be classified in three groups :

- I. Projection fibres.
- II. Association fibres.
- III. Commissural fibres.

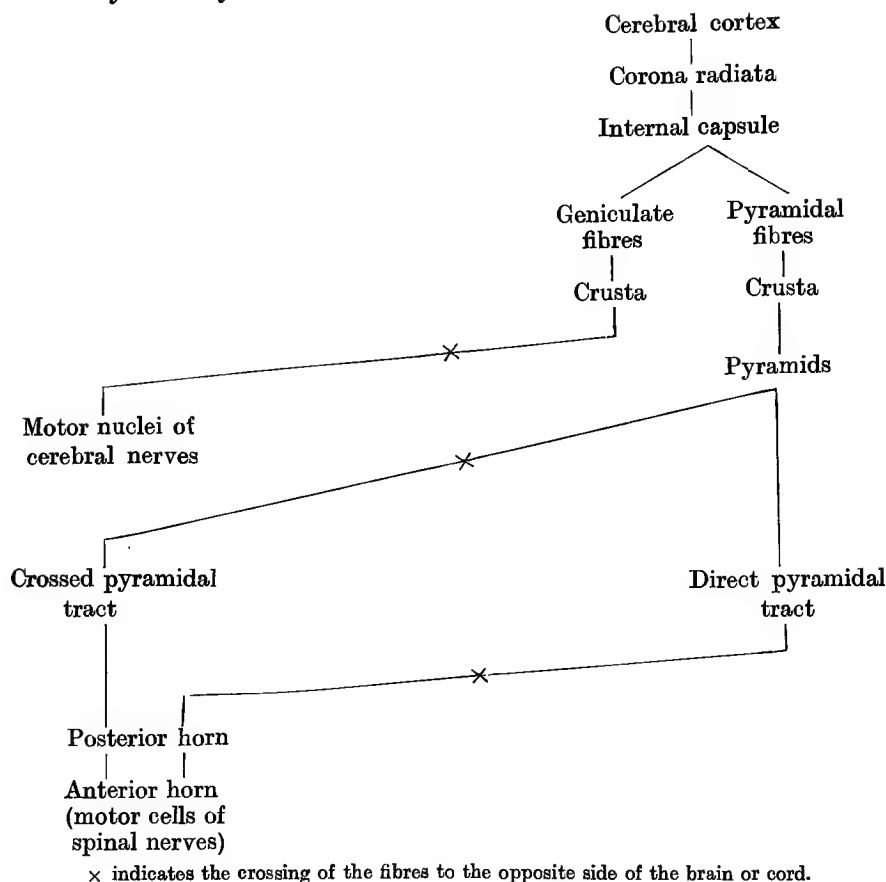
I. Projection Fibres.—The projection fibres connect the cerebrum and cerebellum with the rest of the brain and with the spinal cord. They are of two kinds—descending and ascending.

(a) *Descending.*—The principal descending fibres originate as axons of the pyramidal motor cells of the cerebral cortex. From their origins they converge in the corona radiata to the genu and posterior limb of the internal capsule, and run down through the crustæ of the mid-brain. Those fibres which traverse the genu are termed geniculate, the remainder are the pyramidal fibres (Fig. 66).

The geniculate fibres cross the middle line and arborise around the cells of the nuclei of the motor cerebral nerves of the opposite side of the brain. The pyramidal fibres continue through the pons into the pyramids of the medulla. At the lower end of the medulla they undergo a partial crossing or decussation. The inner fibres, comprising about 75% of the whole, cross to the opposite side and run down in the lateral column of the spinal cord as the crossed pyramidal tract. From this tract, fibres are given off in each segment of the cord to terminate around cells in the posterior horn; the axons of these latter cells arborise in turn around the large multipolar cells of the anterior horn whence the anterior root fibres are derived.

The outermost fibres of the pyramids descend without decussation in the anterior column of the spinal cord as the direct pyramidal tract. In each segment of the spinal cord this tract gives off fibres which cross to the opposite side and terminate around cells of the posterior horn. These, again, communicate with the motor cells of the anterior horn.

This system may be summarised thus :—



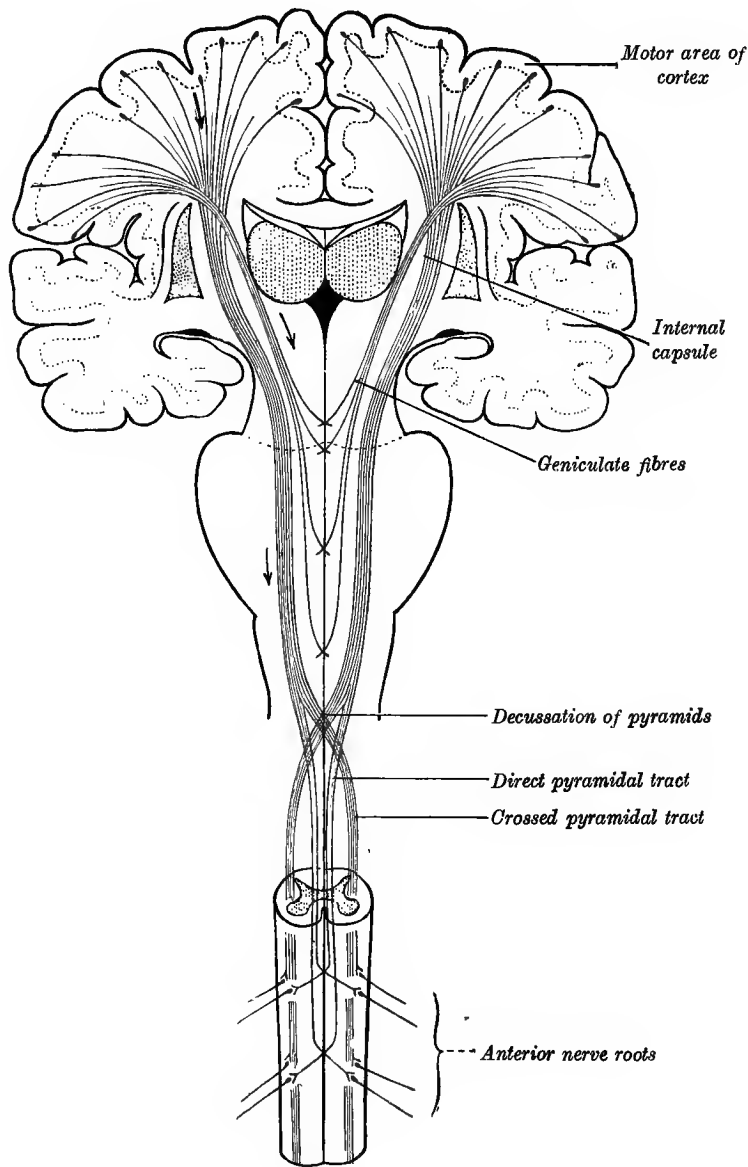
It will be seen that all these motor fibres coming down from the cerebral hemispheres cross to the side opposite to that from which they are derived. If, therefore, their areas of origin on one cerebral hemisphere be stimulated, muscular movements of the other side of the body will be evoked.

In animals, stimulation of one side of the cerebral cortex is followed by a certain amount of muscular movement on the same side of the body, indicating the presence of subsidiary fibres or tracts which do not cross. In man, however, where the pyramidal system is most completely developed, the number of these other fibres is extremely limited.

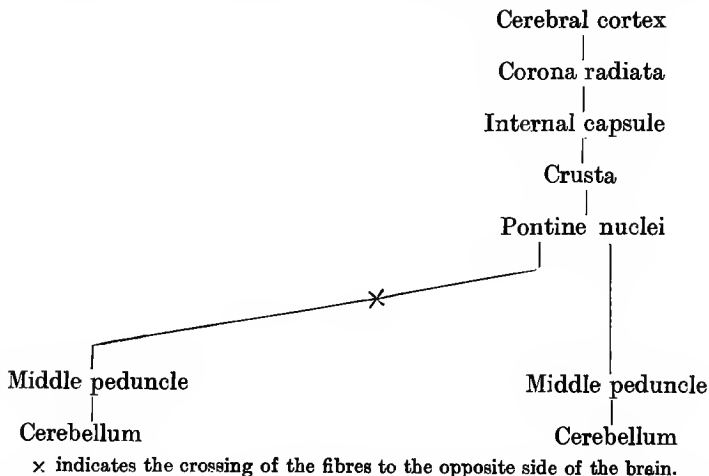
Other descending fibres from the cerebral cortex run with the pyramidal and geniculate fibres through the crusta. They terminate round the small

nuclei pontis; round these same nuclei collaterals from the pyramidal and geniculate fibres also arborise. From the cells of the pontine nuclei new fibre

FIG. 66.—The motor tract. (Modified from Poirier.)



originate and pass either directly or after decussation to the cerebellum by way of its middle peduncles (Fig. 67). This system may be thus represented :



A descending system of fibres from the cerebral cortex runs to the thalamus. New fibres are carried thence, either directly or after interruption in the red nucleus, to the cerebellum through the superior peduncle.

The descending projection fibres from the cerebellum to the spinal cord follow two main routes. One group runs out through the superior peduncle, crosses to the opposite side, and terminates round cells of the red nucleus in the tegmentum; from the red nucleus fibres pass down into the spinal cord. The other set emerges by the inferior peduncle and enters the anterior and lateral columns of the spinal cord (Fig. 68).

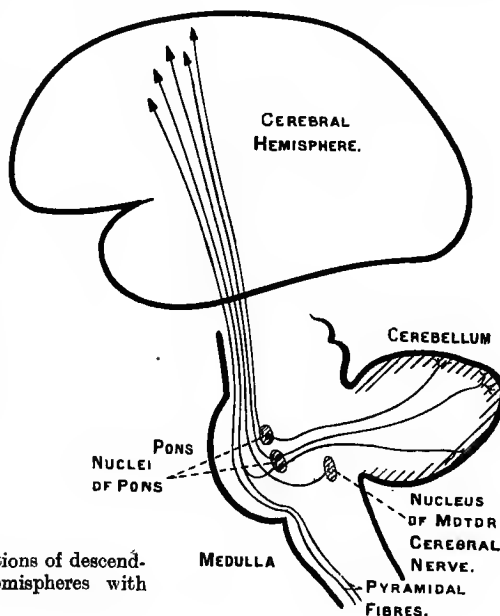
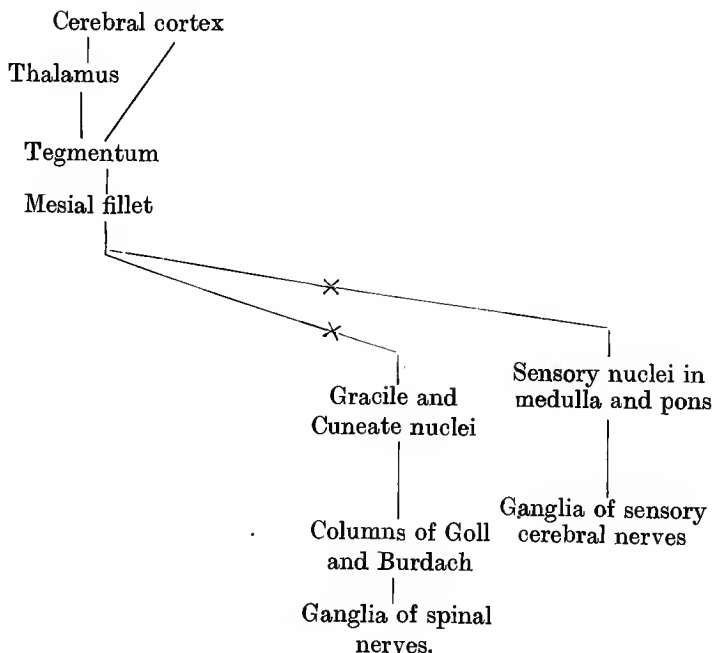


FIG. 67.—Scheme showing connections of descending projection fibres of the cerebral hemispheres with the cerebellum.

(b) *Ascending*.—The ascending projection fibres enter the spinal cord and brain in the first instance from the ganglia on the sensory nerves. As already pointed out the main portions of the entering axons ascend in the cerebro-spinal axis, but large descending branches are also given off.

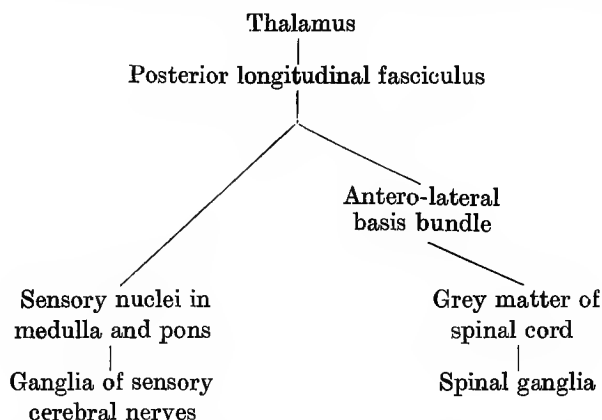
The majority of the axons of the spinal ganglia run up in the columns of Goll and Burdach to the medulla where they end by arborising around the cells of the gracile and cuneate nuclei. From these nuclei new axons arise, cross the middle line and traverse the opposite side of the brain as the mesial fillet (Fig. 69). The entering axons from the ganglia on the sensory cerebral nerves terminate round the cells of the sensory nuclei in the medulla and pons; the axons of the cells of these sensory nuclei cross the middle line and join the mesial fillet of the opposite side. The mesial fillet can be traced through the tegmentum to the thalamus in which most of its fibres end; from the cells of the thalamus fibres radiate to all parts of the cerebral cortex. Some fibres of the mesial fillet pass directly to the cerebral cortex without interruption in the thalamus. Schematically this system may be thus shown :



x indicates the crossing of the fibres to the opposite side of the brain.

All the axons of the spinal ganglia, however, do not run up to the medulla in the columns of Goll and Burdach. Some proceed at once into the grey

matter of the spinal cord. Their further course is extremely problematical, but apparently impulses communicated through them are carried in the antero-lateral basis bundles by various relays of intermediate neurons to the upper part of the spinal cord. Some of these intermediate neurons cross to the opposite side, and others are uncrossed. The antero-lateral basis bundles are continued into the hind-brain as the posterior longitudinal fasciculi which connect up the various nuclei of the cerebral nerves and ultimately reach the thalamus.



A third group of the axons of the spinal ganglia run upwards for a short distance in the column of Burdach and then leave it to arborise round the cells of Clarke's column in the posterior horn. The fibres from Clarke's cells form the direct cerebellar tract which runs up in the inferior peduncle and terminates in the cerebellum. The other well defined ascending projection fibres which enter the cerebellum are: (1) fibres from the spinal cord, entering by the inferior and superior peduncles; (2) fibres from the gracile, cuneate, and inferior olivary nuclei of the medulla, both of the same and of the opposite side; these enter by the inferior peduncle; (3) fibres from the nuclei of the sensory cerebral nerves, also running in through the inferior peduncle.

The only other tract ascending to the cerebral cortex which need be mentioned here is that which originates from the cortex and nuclei of the cerebellum and proceeds upwards in the superior cerebellar peduncle. Many of its fibres terminate directly in the thalamus of the opposite side but some are interrupted in the red nucleus, new axons carrying their impulses thence to the thalamus. From the thalamus radiating fibres run to the cerebral cortex (Fig. 70).

II. Association Fibres.—Although strictly speaking all the fibres of the cerebro-spinal axis bring its several parts into association with one another, yet the term association fibres is reserved for such as connect surface portions

of the same cerebral hemisphere, or of the same cerebellar hemisphere. In the cerebral hemisphere there are numerous fasciculi of association fibres; some of them are short and run between adjacent convolutions, others extend for longer distances between more remote areas of the cortex; they are sufficiently indicated in the diagram (Fig. 71). One of the long association bundles—the fornix—may be mentioned more particularly. The fornix begins in the corpus mamillare and curves upwards behind the genu of the corpus callosum to meet its fellow of the opposite side. The two fornices lie in contact for a short distance, and transverse (commissural) fibres pass between them. The posterior part of the fornix again leaves its fellow, and proceeds downwards and forwards in the descending horn of the lateral ventricle to the hippocampal convolution.

The laminae of the cerebellum are connected with one another by long and short association fibres in a manner similar to the convolutions of the cerebrum.

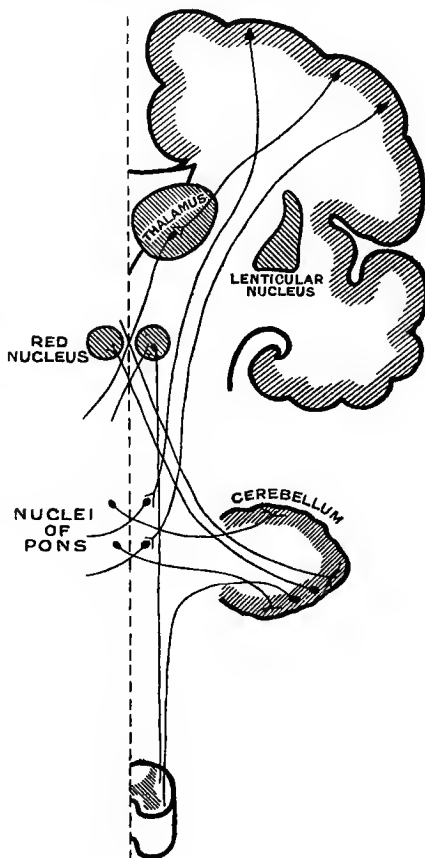
III. Commissural Fibres. —

Along the whole of the spinal cord and brain, fibres are crossing from one side to the other. Many of these are the decussating projection fibres, but others are simple commissural fibres. Thus there are two transverse commissures, an anterior white, and a posterior grey, extending the complete length of the spinal cord and containing fibres of both systems.

In the cerebellum many simple commissural fibres run from one hemisphere to the other through the vermis.

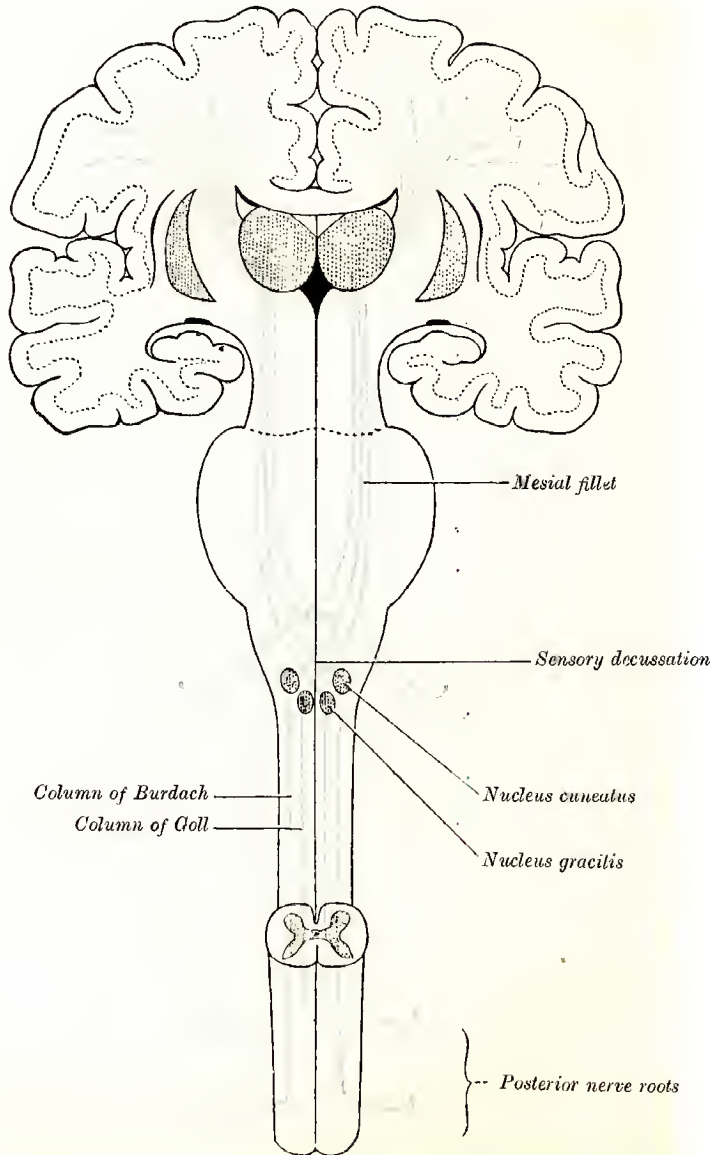
It is in the cerebral hemispheres however that large commissural bands, without projection fibres, can be most clearly differentiated. As already seen the largest of these is the corpus callosum—others of the same nature are the anterior commissure, and, to a lesser extent, the fornix. The fibres of the

FIG. 68.—Scheme showing descending projection fibres of cerebellum. The descending fibres from the cerebral hemispheres to the cerebellum are also shown.



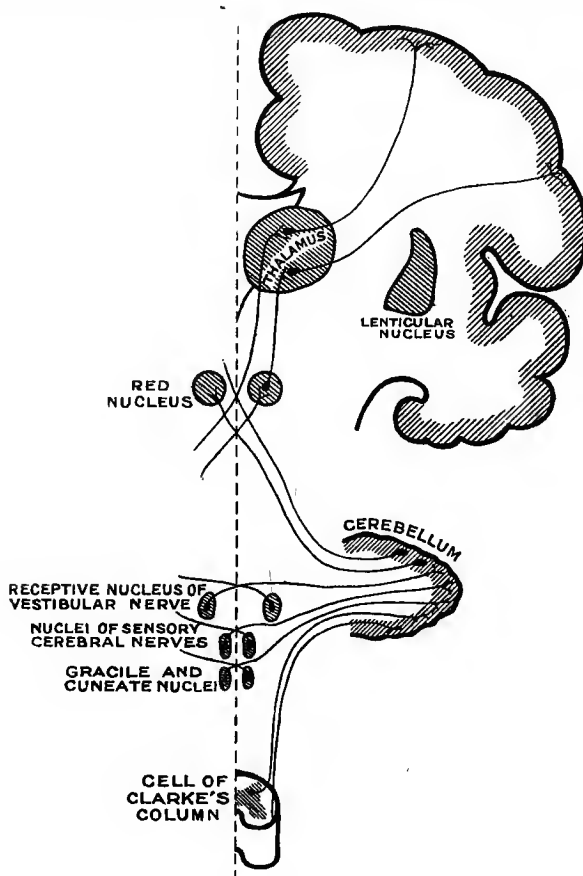
corpus callosum connect the entire cortex of one hemisphere with that of the other (Fig. 72). The anterior commissure joins the temporal lobes of opposite

FIG. 69.—The sensory tract. (Modified from Poirier.)



sides. The transverse fibres of the fornices run from one hippocampal convolution to the other.

FIG. 70.—Scheme showing the ascending projection fibres to the cerebellum. The diagram shows also the ascending fibres from the cerebellum to the cerebral hemispheres.



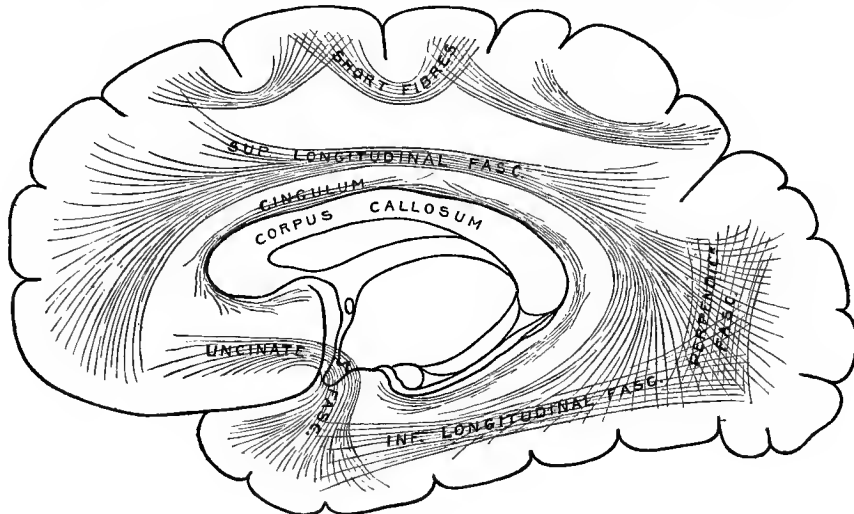
Special Systems

Three of the sensory cerebral nerves, viz. olfactory (i), optic (ii), and auditory (viii), present so much variation from the ordinary arrangement that a special description of them is necessary.

Olfactory.—The term olfactory nerves should, strictly speaking, be limited to a series of fine nerve filaments supplying the olfactory region of the nose. The portion of nervous matter which connects these with the brain is

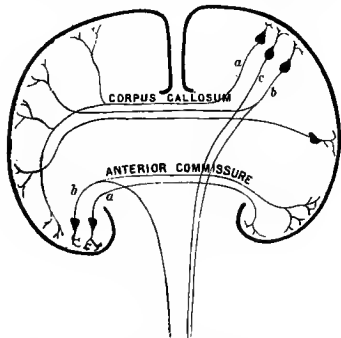
better referred to as the olfactory bulb and tract. The most prominent nerve cells in the olfactory bulb are termed the mitral cells. The dendrites of

FIG. 71.—Diagram showing principal systems of association fibres in the cerebrum.



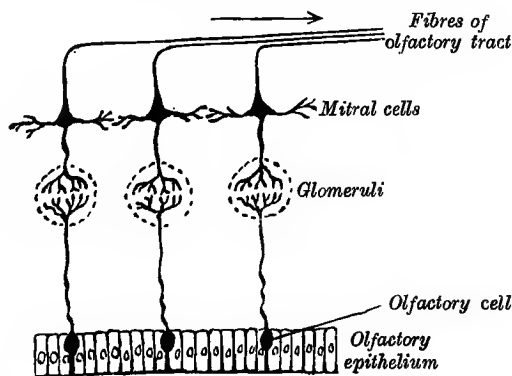
these pass down to meet the entering axons of the olfactory nerves, and at each point of meeting a rich arborisation termed a glomerulus is formed. The axons

FIG. 72.—Scheme of distribution of commissural fibres. (After Cajal.)



a. Simple commissural fibre, *b.* Projection fibre with commissural collateral, *c.* Simple projection fibre.

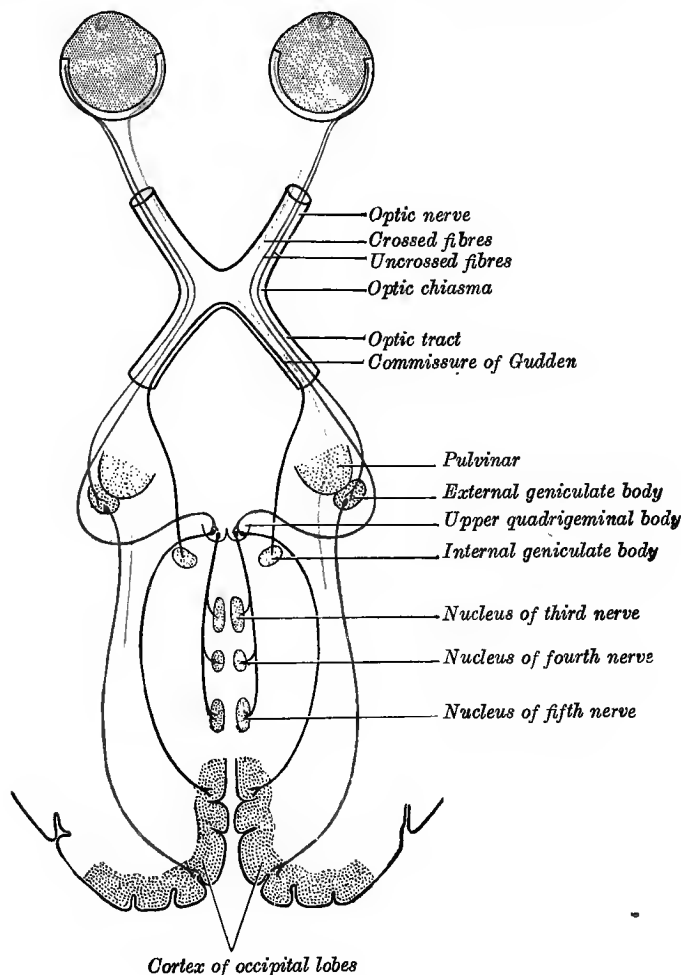
FIG. 73.—Plan of olfactory neurons.



of the mitral cells pass inwards along the olfactory tract to the cerebral hemispheres (Fig. 73). Their connections with the hemispheres are extremely

complicated and are but imperfectly known. Speaking very generally they make their way to the hippocampal convolution mainly in the region of the uncus.

FIG. 74.—Scheme showing central connections of the optic nerves and optic tracts.

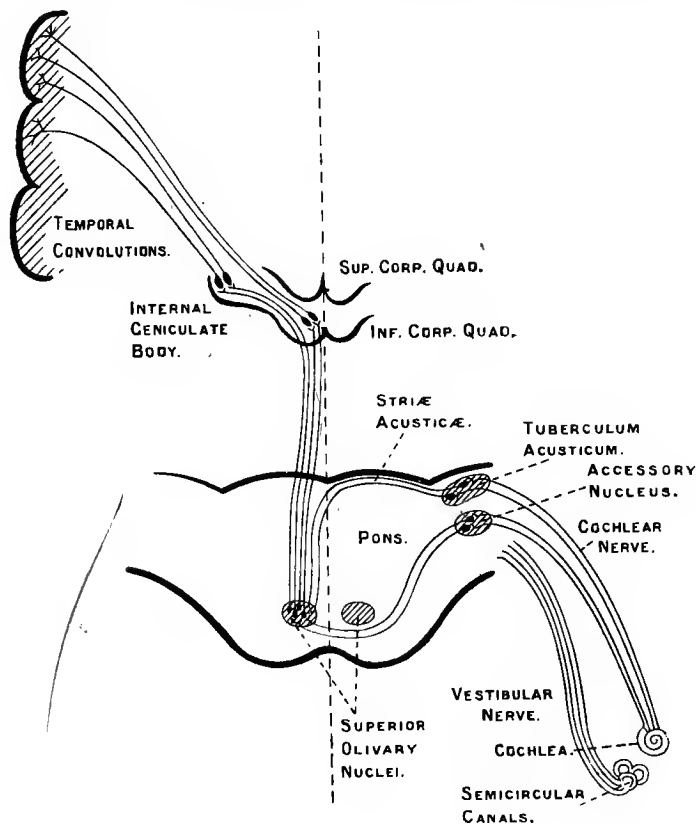


Some pass to the uncus of the same side ; others cross in the anterior commissure to that of the opposite side.

Optic.—The fibres of the optic nerves are almost entirely axons of cells of the retina ; they run back to the optic chiasma where they undergo a partial decussation. The fibres from the inner or nasal side of the retina cross in the

chiasma to the optic tract of the opposite side ; the fibres from the outer side of the retina are continued into the optic tract of the same side. The optic tract on either side passes upwards and backwards towards the posterior end of the thalamus. Some of its fibres terminate in the pulvinar, some in the external

FIG. 75.—Scheme showing the central connections of the cochlear nerve.



geniculate body, while others are continued along the superior brachium to the superior quadrigeminal body. These parts are spoken of as the lower visual centres. From them new fibres originate and ascend in the hinder end of the internal capsule to the cortex of the occipital lobe (Fig. 74).

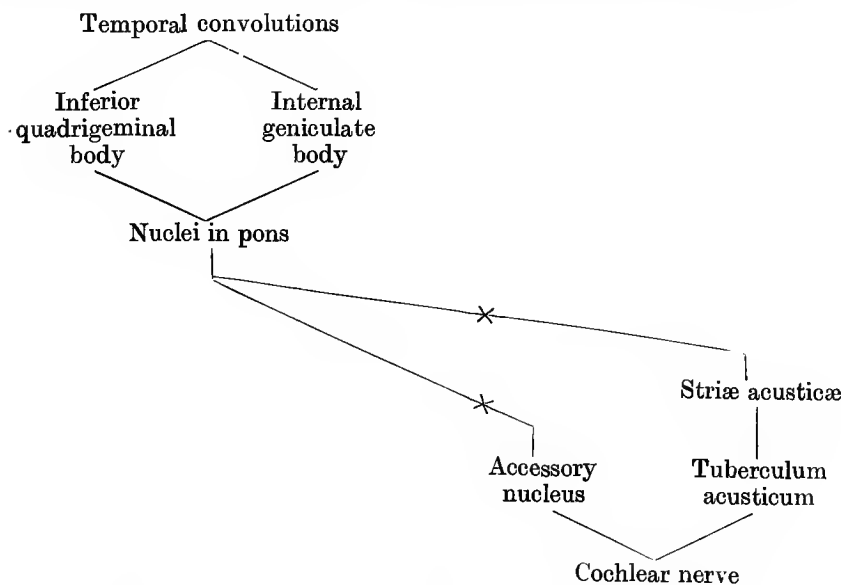
Auditory.—The auditory nerve consists in reality of two functionally distinct nerves. One—cochlear division—originating in the cochlea, the organ of hearing, conveys the sensations of sound ; the other—vestibular division—

from the semicircular canals, conveys impulses which regulate muscular activities associated with equilibrium.

Cochlear Division.—The fibres of the cochlear division are the axons of the cells of a ganglion situated within the cochlea. They pass first to two nuclei lying at the side of the medulla—the tuberculum acusticum and the accessory auditory nucleus. The fibres arising from the tuberculum acusticum run inwards across the floor of the fourth ventricle as the *striæ acusticæ* (p. 51), and dip into the substance of the pons, some to the same side, others crossing the mid-line. Most of them arborise round the superior olive and pontine nuclei, and the pathway is continued by new fibres into the lateral fillet (Fig. 75).

The fibres from the accessory nucleus pass directly into the substance of the pons. Some run up on the same side, others cross to the opposite side. Many of them terminate round the cells of the superior olive, and, as before, the pathway is continued through the lateral fillet. Many fibres from both auditory nuclei are not interrupted in the nuclei of the pons but proceed directly into the lateral fillet.

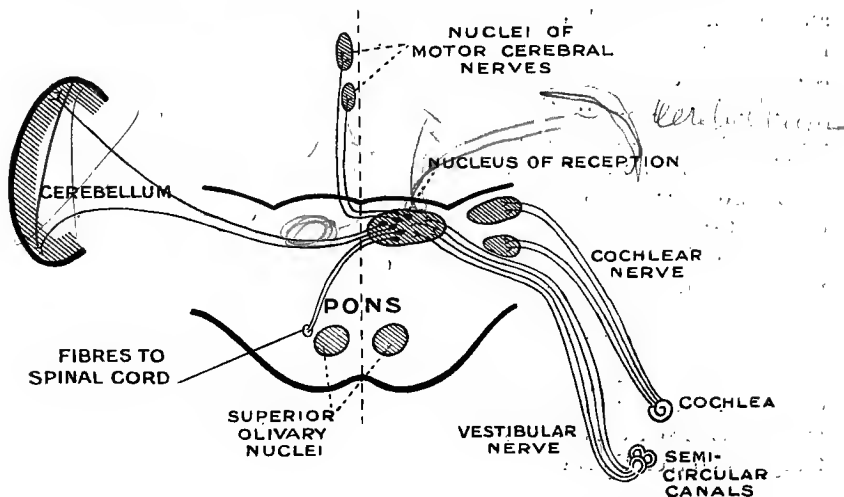
If the lateral fillet of one side be traced it will be found that some of its fibres terminate in the cells of the inferior quadrigeminal bodies, others pass out by the inferior brachium to the internal geniculate body. The new fibres which arise from these regions form a band that proceeds to the cortex of the temporal convolutions through the posterior part of the internal capsule.



x indicates the crossing of the fibres to the opposite side of the brain.

Vestibular Division.—The fibres of the vestibular division are the axons of cells of a vestibular ganglion situated close to the internal ear. They pass into the floor of the fourth ventricle where most of them terminate round the cells

FIG. 76.—Scheme showing central connections of the vestibular nerve.



of a large complex nucleus of reception. From this nucleus new fibres run to form communications with the nuclei of the motor cerebral nerves, with the spinal cord, and with the cerebellum (Fig. 76). No fibres have been traced into the cerebral hemispheres.

CHAPTER IX

THE AREAS OF LOCALISATION ON THE CEREBRAL CORTEX

OF all portions of the brain the cerebral cortex possesses the most direct interest to the psychologist. In it the afferent and efferent arms of the long reflex pathways, which represent the highest type of reflex arcs, meet, and in it also many sensations are mediated. Further it is the region where consciousness and memory are located, and where the complex nervous processes which find expression in the highest forms of psychical activity take place.

From the manner in which the nervous system has gradually progressed to its great complexity in the higher animals, it is obvious that different portions of it are specialised for different functions. This general localisation was all that was known to the older physiologists, who recognised that the spinal cord presided over the execution of movements, that the cerebellum was concerned in their co-ordination, and that in the upper parts of the brain voluntary movements were initiated.

It is only since 1870 that direct proof of the functional differences between different areas of the cerebral cortex has been advanced. The first result of this work led to the belief that the cortex could be mapped out into small areas anatomically independent of one another and differing in physiological function. Later experiments and observations have shown that although there are marked differences of function between individual parts of the cortex, yet every part of the cortex is so intimately connected with every other portion that such independence is only relative. In other words interference with one part will produce effects in several other regions. This applies even to such widely different functions as sensation and motion, for in the cortex the neurons of these are so intimately associated that an insensible transition from one to the other is effected.

Three methods have given valuable results in the study of cortical localisation: (1) Physiological; (2) Histological; (3) Clinical.

(1) *Physiological*.—The first convincing experiments performed in animals were those of stimulation of different areas of the cortex. The cortex was exposed by removal of a portion of the skull, and stimulated electrically. By this method a region was demarcated, stimulation of portions of which evoked definite muscular movements, and the presence of a motor area was thus established.

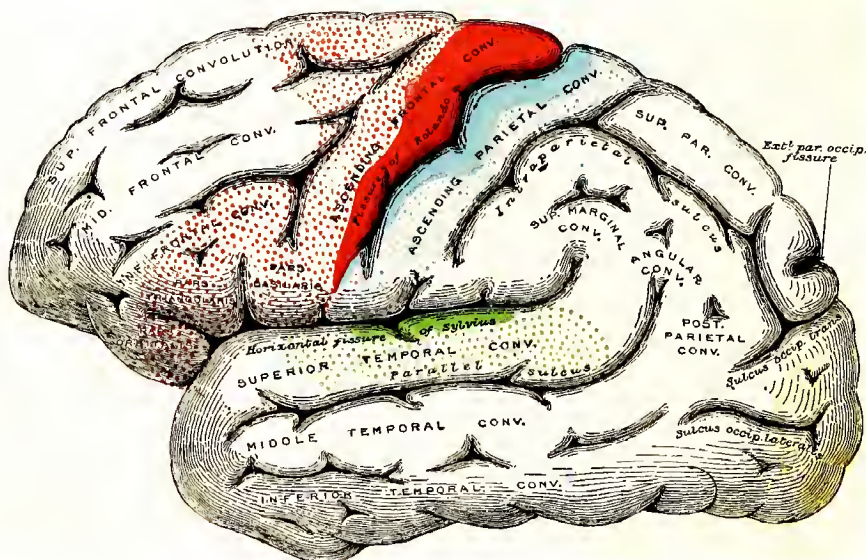
Previous to this the chief mode of experimenting was by removing or

destroying portions of the cortex, and then after a time carefully examining the voluntary muscular paralyses or interferences with sensation which followed. By a combination of the two methods greater accuracy has been ensured.

In a third series of experiments, portions remote from the cortex were destroyed, and the resulting changes (if any) in the cortex noted.

(2) *Histological*.—The older method of histological investigation is an extension of that already described (p. 31) in connection with the tracing of the

FIG. 77.—Areas of localisation on outer surface of hemisphere.



Motor area in red. Area of general sensations in blue. Auditory area in green. Visual area in yellow. The dotted regions represent the psychic portions of the respective areas.

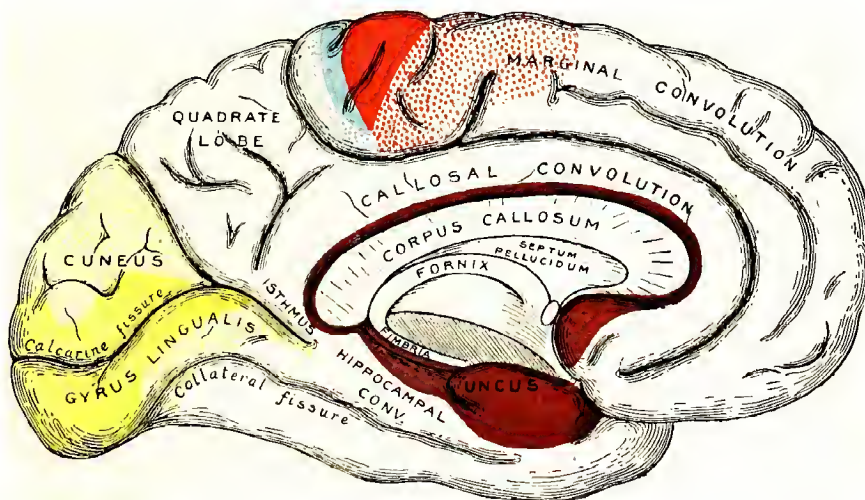
nerve tracts, viz. observing the different periods at which the white fibres running to and from known areas of the cortex acquire their medullary sheaths.

While it had been known for some time that the types of cells and their arrangement in layers were not exactly alike in all the regions of the cortex, yet it is only within the last few years that careful systematic observations have been made to determine whether these differences had any definite relation to cortical localisation. It has now been shown that such a relationship does exist; certain areas can be accurately differentiated by microscopic examination of their characteristics, but the proof of their functions necessarily rests on the other methods. Much has yet to be done in this direction.

(3) *Clinical*.—In man, and to a lesser extent in animals, important information has been gained by studying the effects of known injuries and diseases of

the brain. Destruction of the cerebral cortex may be due to external injuries, to abnormal growths, or frequently to the rupture of bloodvessels within the skull, and in such cases the amount of injury can be determined roughly by naked-eye inspection; in a crude manner motor and sensory areas may be thus delimited. In cases of obscure nervous diseases or of mental affections, no gross surface differences may be observable; the great motor and sensory tracts may be but little affected, although all the higher psychical activities are

FIG. 78.—Areas of localisation on mesial surface of hemisphere.



Motor area in red. Area of general sensations in blue. Visual area in yellow. Olfactory and gustatory areas in purple. The dotted regions represent the psychic portions of the respective areas.

interfered with. The recent methods of studying, microscopically, the intimate structure of the cortex in these cases has added much to our knowledge.

By the use of these various methods, singly or in combination, it is possible to map out on the surface of the cerebral cortex certain areas with well-defined functions—thus, motor areas, sensory areas, and association areas are described. The motor areas have been determined with much accuracy; some of the sensory areas are also well known; the association areas, necessarily from their great complexity, are as yet but imperfectly understood. In a general way the cortex in front of the Rolandic fissure may be regarded as the great efferent area, while the rest of the cortex is specialised for the reception of sensory impressions. It must not be forgotten, however, that the motor area has many afferent (but not sensory) fibres, and it is by impulses through these that the motor cells are thrown into activity; hence the motor area is more accurately designated the psycho-motor area (Figs. 77 and 78).

Motor Area.—The motor area is situated immediately in front of the fissure of Rolando, occupying the greater part of the precentral convolution, and extending for a short distance into the hinder ends of the superior, middle, and inferior frontal convolutions and on to the mesial surface of the hemisphere. In this large area, individual regions can be recognised representing groups of associated movements. Thus the areas for the head and neck movements are situated at its lower end ; for the arm and trunk movements about its middle ; for the leg at the upper end and adjacent part of the mesial surface.

Sensory Areas.—The sensory areas so far as they have been differentiated comprise (a) an area for general body sensibilities, i.e. the senses of pressure and temperature, and the muscular senses ; (b) a visual area ; (c) an auditory area ; (d) an olfactory and gustatory area. Each area is of a dual nature : one portion is purely sensory receptive and mediates the appropriate sensation ; the other portion is psychic or associational and is the region where the specific sensori-memorial images are combined and stored.

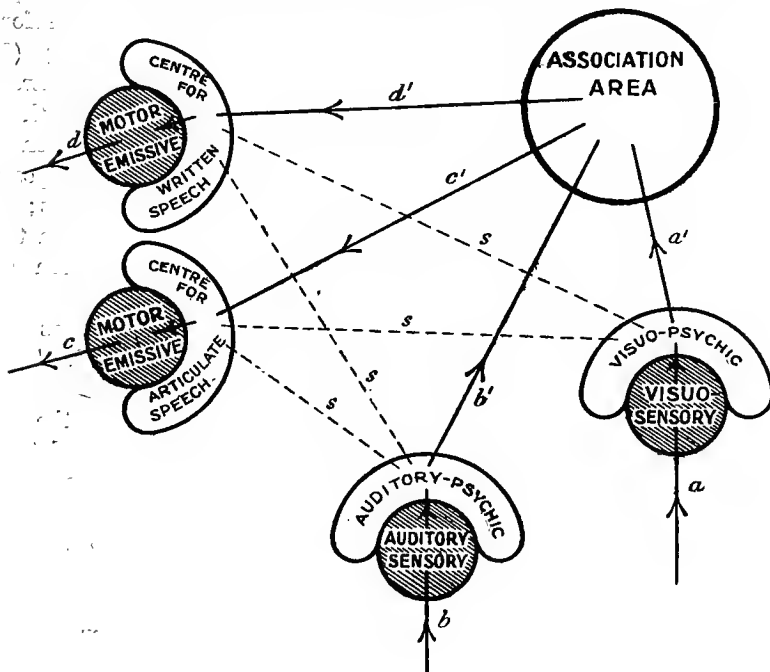
(a) The region immediately behind the Rolandic fissure, i.e. the post-central convolution and the parts adjacent to it, constitute the sensory area for the general body senses. No area associated with the sense of pain has as yet been found. (b) The visuo-sensory area is situated on the lips of the calcarine fissure. The visuo-psychic portion extends over the cuneus and gyrus lingualis and on to the greater part of the outer surface of the occipital lobe. (c) The auditory-sensory area occupies the middle third of the superior temporal convolution ; the greater part of the rest of the superior temporal convolution represents the auditory-psychic region. (d) The olfactory area is placed by most observers on the hippocampal convolution especially in the region of the uncus. The area for the gustatory sense has not been satisfactorily determined, but is supposed to lie also on the hippocampal convolution behind the olfactory area.

Association Areas.—When all the motor and sensory areas have been marked off, a considerable portion of the cortex still remains. This remainder consists of areas called association areas in which, it is supposed, elaborated impressions arrive from all the sensory areas and are combined into perceptions and conceptions. Four association areas are usually described : (1) frontal, immediately anterior to the motor area ; the part of this region which forms the frontal pole is delimited as a special area, the prefrontal ; (2) parietal, between the general sense area and the visual area ; (3) temporal, occupying the greater part of the temporal lobe ; (4) insular, the island of Reil. Of these the prefrontal is the last to be formed and is supposed to be concerned with all the highest and latest acquired cerebral functions. In cases of insanity it is the region which is specially affected.

In the description of the cerebral cortex (p. 66) it was pointed out that five typical layers of cells and fibres entered into its structure. These vary in relative thickness in the separate functional areas. By careful study of

their development and arrangement, certain views as to their functions have been formulated. Thus the outer cell lamina is said to subserve the psychic or associational functions of the brain, and is found best developed in the

Fig. 79.—Scheme to show the areas involved in the language mechanism.



- Injury to ingoing fibres *a* results in blindness.
 " " " " *a'* " " word-blindness.
 " " " " *b* " " deafness.
 " " " " *b'* " " word-deafness.
 " " outgoing " *c'* results in motor apasia.
 " " " " *c* " " paralysis of muscles of articulate speech.
 " " " " *d'* " " motor apasia.
 " " " " *d* " " paralysis of muscles of written speech.
 a. Secondary paths between the sensory and motor areas.

association areas. The middle cell lamina receives and transforms afferent impressions; it is well marked in the sensory areas. The inner cell lamina is concerned in the lower voluntary and instinctive activities; it is the most important layer in the cortex of the lower animals.

The Language Mechanism.—The study of the mechanism of language involves a summary of all the higher functions of the brain. Amongst animals, and in man, a series of motor actions is used to express the emotions, and serves as a mode of communication; this may be regarded as a lowly form of language. In the usual interpretation of the term, however, language is

regarded as a purely human characteristic which is exhibited in two forms, viz. articulate speech and written speech. The sequence of events in the language mechanism is: impressions derived from external objects evoke sensations; sensations are combined into ideas which are converted into the form of words; these are transferred to the motor mechanism, and expressed as articulate or written speech. The following cortical areas therefore are called into requisition: (1) one or more sensory receptive areas; (2) the corresponding sensory psychic areas; (3) association areas; (4) areas for articulate or written speech; (5) motor emissive areas. The second, third and fourth of these groups represent the language areas, and any interference with them results in a condition known as aphasia. For practical purposes the most important are: (a) the auditory-psychic and visuo-psychic areas; (b) the posterior (parietal and temporal) association areas; (c) the areas on the left frontal lobe for articulate speech (Broca's area) and for written speech (Fig. 79).

In certain diseases of the cerebrum, one or more of these areas may be affected, and thus several varieties of aphasia may be recognised. The first great division is into sensory and motor aphasias.

Sensory Aphasia.—If the auditory-psychic area be damaged, the patient is still able to hear spoken words but is quite unable to understand them—a condition known as word-deafness. It must be clearly understood that the patient is not deaf; he can hear ordinary sounds quite well, but spoken words with which he was formerly perfectly well acquainted, become to him like the words of an unknown language.

Similarly when the visuo-psychic area is damaged word-blindness results; the patient can see the written or printed words, but cannot comprehend them.

When the association areas for the combination of the sensori-memorial images from these regions are affected, the patient can still hear and see the words but cannot resolve them into ideas, and thus cannot express them.

In cases of pure sensory aphasia, the ability to speak and write in a mechanical manner is still retained by the patient, i.e. he can repeat words spoken to him, or can copy from manuscript, or write from dictation.

Motor Aphasia.—The centre for articulate speech was localised by Broca in the hinder end of the inferior frontal convolution. As all the great efferent paths are crossed, this centre is situated on the left hemisphere in right-handed individuals and on the right in left-handed people. Up till recently the proofs of the function of Broca's area were regarded as conclusive. It may be again emphasised that this area was not regarded as the motor centre for the muscles of speech; a patient suffering from motor aphasia may be able to pronounce words, but they are not the words suitable to his thoughts and he is often aware that he has said something quite absurd and foreign to the subject he wishes to indicate. In a similar way the centre for written speech was said to be localised immediately above the area of Broca.

Marie, however, has thrown great doubts on these views and has adduced evidence to show that all forms of aphasia are due to interference with the posterior association areas. In those forms where the patient is unable to produce articulate speech there is an additional injury in the region of the lenticular nucleus ; this is the only injury that can cause pure motor aphasia. Motor aphasiae are due therefore to a combination of a cortical injury in the posterior association areas (aphasia proper) and a sub-cortical injury (anarthria). As a corollary to this, aphasia is always associated with an impairment of the intellectual powers.

CHAPTER X

THE SENSE ORGANS

EVERY sensation arises from the stimulation of a particular form of nervous mechanism known as a sense organ. In the widest acceptation of the term, a sense organ comprises: (1) receptive cells, to which the stimulus is applied; (2) sensory neurons, conveying the impulse towards the cerebro-spinal axis, (3) one or more secondary relays of sensory neurons, which carry the impulse to a special region of the brain, usually of the cerebral cortex. It is generally believed that the character of the sensation depends entirely on the last of these neurons (p. 15).

The function of the receptive cells is to pick out from the mass of different stimuli constantly arriving, those to which the specific sense organ is attuned. The recognition of a sensation is an act of consciousness, and is usually made without effort; there are, however, certain forms of sensation, notably in connection with the muscular apparatus, which are not appreciated by those uneducated to analyse them, and may therefore be classified as sub-conscious.

Two important facts in connection with sensations may be noted here: (a) a sensation is not only perceived but can also be localised, either to a part of the body or to a distant object emitting the stimulus; (b) within certain limits the intensity of the sensation bears a direct proportion to the strength of the stimulus. In experimenting on this, Weber measured the amount of increase of stimulus which produces a just appreciable increase in the sensation. As a result of his observations he formulated the law that 'the increase of stimulus required to produce a distinct increase of sensation always bears the same ratio to the whole stimulus.' The ratio varies for different sensations, but is constant for any one particular sensation. To take an example; the ratio for the pressure sensation is 1 : 30, so that if a weight of 30 grams be hung on the finger, no difference will be detected in the sensation until one gram more is added. Fechner, by making the assumption that the just appreciable differences in sensation are equal in amount, elaborated Weber's law into the following: 'if the stimulus increases by a certain multiple (geometrical progression) the sensation increases by regular additional amounts (arithmetical progression)'; this is known as the psycho-physical law.

In the older classification of sensations five were recognised, viz. sight, hearing, taste, smell, and touch. Modern methods of analysis have, however,

shown the presence of many other forms such as temperature, pressure, pain, and the various static sensations. Several internal sensations, e.g. hunger, thirst, etc., are also recognised, but these are extremely difficult to define.

In the preceding chapters the pathways of the neurons from the receptive cells to the cerebral cortex have been traced. It remains to describe the receptive portions of the sense organs.

The Eye

The essential receptive part of the organ of vision is a delicate membrane composed of several layers of nerve cells, and known as the retina. Accurate images of external objects are thrown on this membrane by means of a series of dioptric mechanisms. The whole apparatus is incorporated in a globular structure, the eyeball.

The human eyeball is made up of segments of two spheres, one in front of the other. The posterior sphere, which is the larger, forms about five-sixths of the eyeball; it contains a transparent jelly-like substance, the vitreous humour. The anterior sphere constitutes about one-sixth of the eyeball; it projects forwards, and within it is a watery fluid termed the aqueous humour. Between the aqueous humour and the vitreous humour is a transparent biconvex body, the lens (Fig. 80).

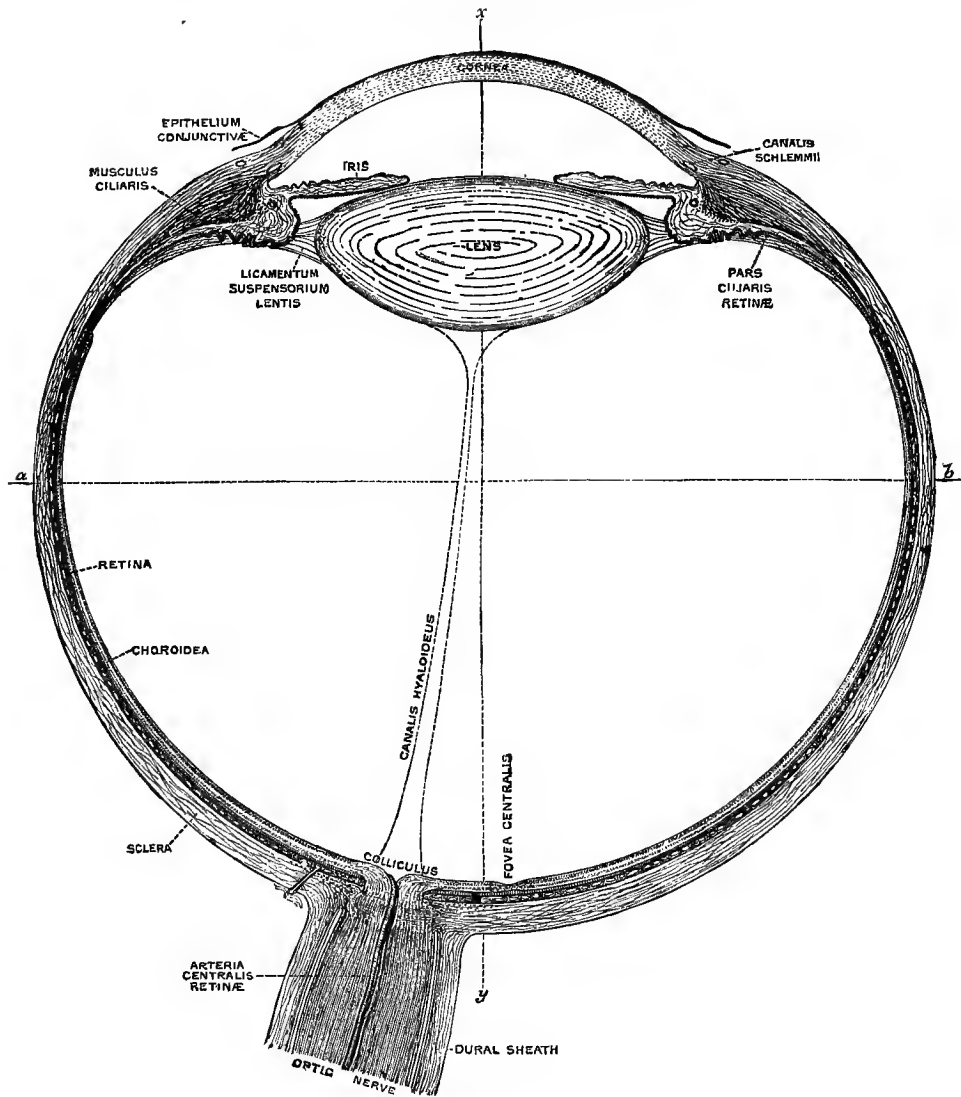
The wall of the eyeball consists of three coats or tunics named from without inwards: (1) the fibrous tunic, composed of the sclera and cornea; (2) the vascular tunic, consisting of the choroid, ciliary body, and iris; and (3) the nervous tunic, the retina.

(1) The *sclera* forms the posterior five-sixths of the outer tunic; it is tough in texture, opaque, and white in colour. The *cornea* is the projecting anterior part of the outer tunic; it is continuous with the sclera, the line of junction being practically circular. Unlike the sclera, however, it is transparent, and forms one of the refracting media of the eye.

(2) The posterior part of the vascular tunic is loosely adherent to the sclera and is known as the *choroid*. It consists largely of an interlacement of small bloodvessels, and contains also cells charged with a brownish-black pigment. The anterior part of the vascular tunic hangs free behind the cornea, as the *iris*, a circular curtain or diaphragm; a little to the nasal side of its centre is the rounded aperture of the pupil. The iris gives the characteristic colour to the eye and varies, therefore, in different individuals; the colour is due to cells containing a brownish-black pigment, and the amount and distribution of this determines the tint. In the substance of the iris, muscular fibres are arranged in two groups, circular and radiating. The aperture of the pupil diminishes in size when the circular fibres contract, while contraction of the radiating fibres dilates it. Between the choroid and iris is an intermediate portion called the *ciliary body*; it is thrown into a series of folds—the ciliary

processes—which are closely connected to a ligament (suspensory ligament) round the lens. Within the ciliary processes are numerous muscular fibres ;

FIG. 80.—Diagram of right adult human eye—divided nearly horizontally through the middle. (E. A. Schäfer.) Enlarged.



xy. The optic axis.

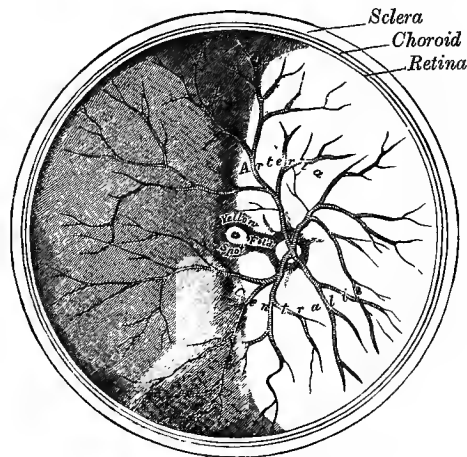
when these contract they pull the ciliary body forwards and relax the suspensory ligament of the lens.

(3) The *retina*, the innermost tunic of the eyeball, is closely applied to the choroid, and extends forwards on to the back of the ciliary processes and iris. The nerve cells, which are its chief characteristic, are found only in the posterior portion extending forwards almost to the ciliary processes. The margin between the nervous and non-nervous portions is jagged in outline and is termed the *ora serrata*. In the centre of the posterior segment of the retina is a small oval area with a yellowish tinge—the yellow spot¹ (*macula lutea*) ; within this area is a central depression, the *fovea centralis*. About 3 mm. to the nasal side and 1 mm. below the level of the yellow spot is a slight elevation which marks the area of entrance of the optic nerve (Fig. 81).

The structure of the retina is very complicated, but for practical purposes it may be said to consist of three layers of bipolar neurons, interlacing with supporting structures and cells of association (Fig. 82). The terminal neurons, applied to the choroid, are specially modified to receive the light waves, and exhibit two forms, viz. rods and cones. The rods are cylindrical thickenings of the dendrites, and project backwards at right angles from an outer limiting membrane; the cell bodies are situated a little distance in front of this membrane. The cones are somewhat flask-shaped thickenings of the dendrites, with their bases resting on the outer limiting membrane; the cell body is in contact with the base of the cone. Between the stratum of rods and cones and the choroid is a layer of pigmented cells, processes from which extend between and envelop the rods and cones.

The axons of the rod bipolars and cone bipolars pass into the substance of the retina and meet and arborise with the dendrites of the second layer of neurons. The axons of these in turn run towards the internal surface of the retina to arborise with a layer of large ganglionic cells. The axon fibres,

FIG. 81.—The posterior half of the eyeball viewed from the front.

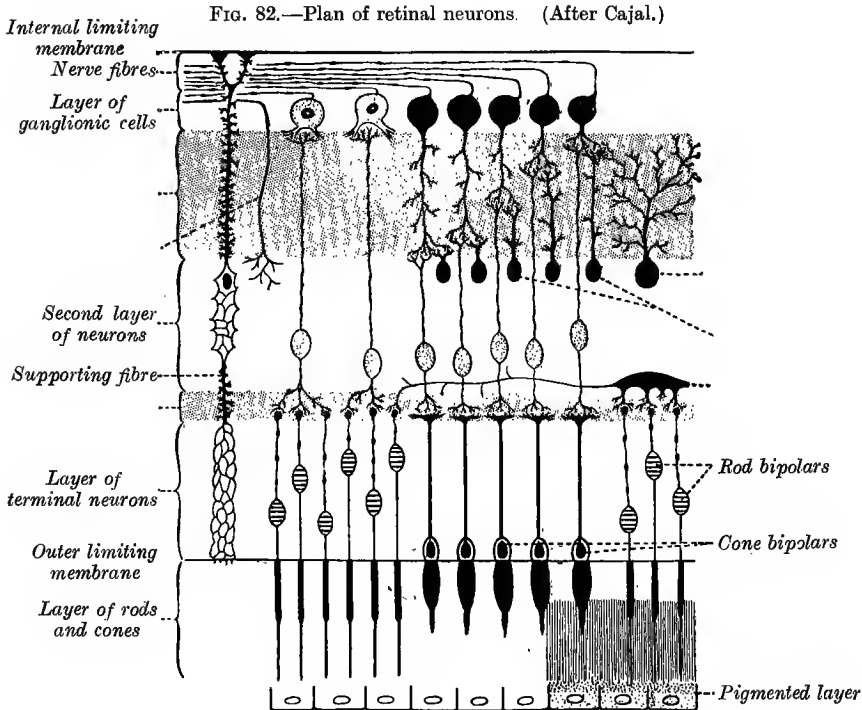


The artery is emerging from the area of entrance of the optic nerve.

¹ Recent observers hold that the yellow colour appears only after death and that there is no indication of it during life.

derived from the latter, form the optic nerve and are carried to the cerebrum in the manner already described (p. 77).

In the yellow spot all the layers except the layer of the rods and cones and the layer of ganglionic cells (which is actually increased) are reduced in thickness. In the fovea centralis, only the terminal neurons are present and these are entirely cone bipolars.



Refracting Media.—There are four refracting media in the optical mechanism of the eye : (1) the cornea, already described ; (2) the aqueous humour, a dilute saline fluid in the anterior segment of the eyeball—the refractive powers of this and the cornea are so nearly alike that they practically form one medium ; (3) the vitreous humour, an albuminous fluid, enclosed in a fine membrane, and occupying the posterior segment ; (4) the lens. The lens is a transparent, biconvex structure enclosed within an elastic membranous capsule. The convexity of the anterior surface is less than that of the posterior but both are influenced by the tension of the capsule ; thus if the capsule be relaxed the convexity of the lens is increased but more particularly that of the anterior surface. The membrane that encloses the vitreous humour is intimately

applied to the ciliary processes, where it is somewhat thickened and is termed the zonule of Zinn. A lamina derived from this is attached to the capsule of the lens and forms its suspensory ligament (Fig. 83); when, therefore, the zonule is drawn forwards by the ciliary muscle the lens capsule is relaxed.

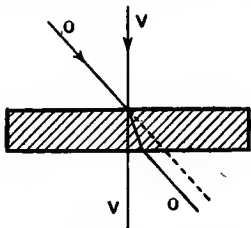
The Optical Mechanism of the Eye.—In its general structure the eyeball resembles a photographic camera—the retina being the sensitive plate. In place of a single lens, however, there are several refractive media, and focussing is effected, not by altering the distance between lens and plate, but by changing the curvature of the lens.

Some of the more simple facts regarding the formation of images by biconvex lenses may be mentioned. When an oblique ray of light leaves a medium of low density such as the ordinary atmosphere, and enters a more dense medium, e.g. glass, it is bent or refracted from its course (Fig. 84). If it completely traverses this dense substance it undergoes two refractions, one on entering, the other on leaving. When the ray enters at right angles to the surface it is not refracted.

If the glass be formed in the shape of a biconvex lens, parallel rays of light falling on it are refracted so as to meet at a point termed the principal

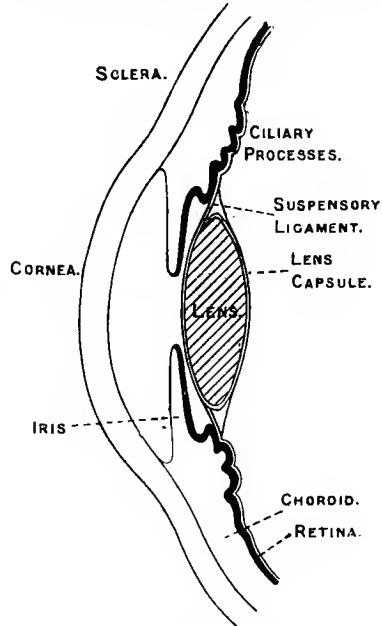
focus; the distance of this point from the lens is the focal length (Fig. 85). Similarly, rays of light emitted from a point situated at a distance equal to the focal length emerge as parallel rays. When the rays falling on the lens are not parallel, but are derived from a source of light a little beyond the focal length, they are brought to a focus at a point beyond the principal focus; if from a source nearer than the focal length, the emerging rays are divergent and are not focussed. Within every

FIG. 84.—To show the manner in which an oblique ray of light O is refracted in passing through a denser medium.



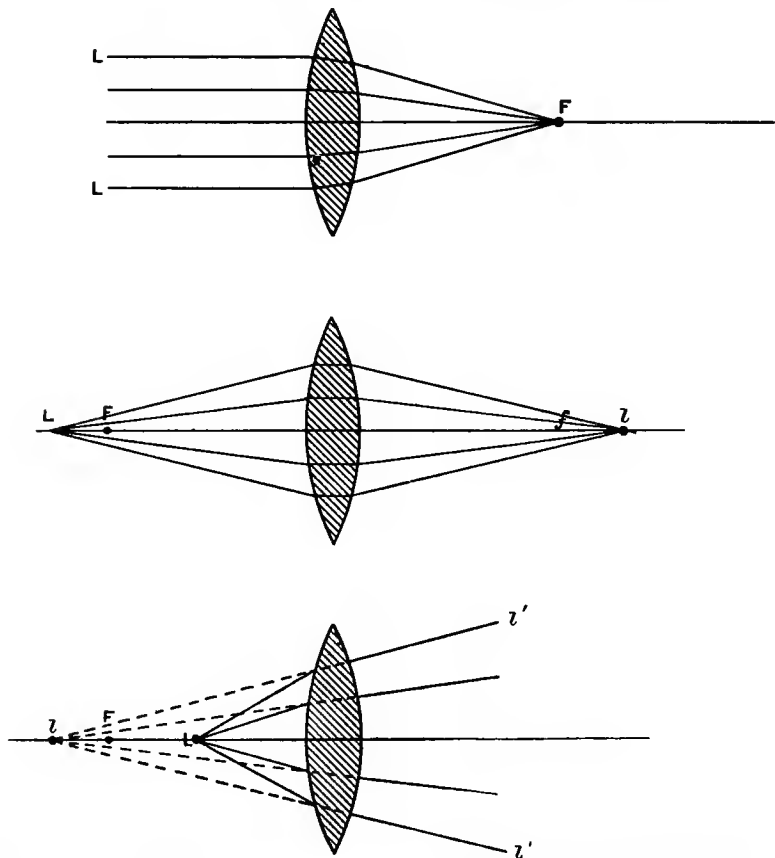
biconvex lens is an imaginary point called the optical centre, and rays of light passing through this do not undergo refraction. The method of determining

FIG. 83.—Diagram of vertical section through front of eyeball to show connections of suspensory ligament of lens.



the position of the image of a simple rod is shown in Fig. 86. Parallel rays of light from a are refracted to pass through the principal focus F ; rays through the optical centre O are not refracted. The point of intersection of the lines

FIG. 85.—Diagrams showing refraction of light L by a biconvex lens.



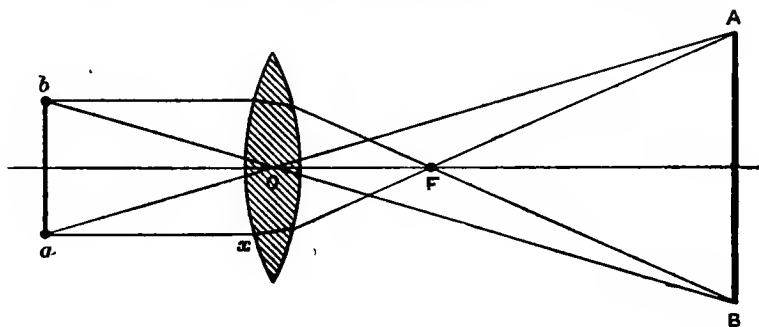
In the uppermost figure parallel rays are brought to the principal focus F . In the middle figure convergent rays from a source outside F are focussed at a point l beyond the focal length (indicated by f). In the lowermost figure converging rays from a point within F are not focussed, but become divergent.

aO and aF is the image of a . Similarly the image of b is determined. It will be seen that the image is inverted and that its size is proportional to the distance of the object from the lens.

When a ray of light enters the front of the eye it undergoes refractions at the several refractive media; in the normal eye at rest, parallel rays of light are brought to a focus on the yellow spot of the retina. Practically all objects

farther distant from the eye than twenty feet may be considered as emitting parallel rays so that they are brought accurately to a focus without effort on the yellow spot. If the eye remained at rest, an object nearer than twenty feet would be focussed behind the retina, and its image on the retina would therefore be blurred. This is obviated by increasing the convexity of the lens through the action of the ciliary muscle as already described. The effect of the increased convexity is to refract the rays of light through a greater angle and thus bring the image forward on to the retina. This is known as accommodation, and the mechanism is effective for objects up to a distance of about five inches. The image on the retina is of course inverted, but the brain takes no cognisance of this fact; in other words the brain does not realise the image, but projects it back to the object from which it is derived.

FIG. 86.—Construction to find the image A B of a simple rod *b a*.



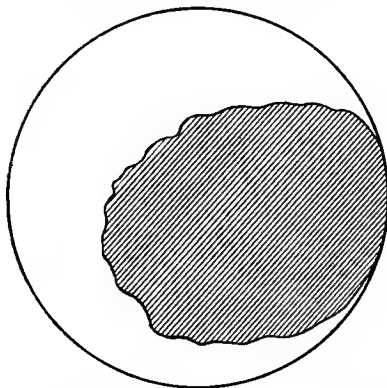
Optical Defects of the Eye.—The refractive media of the eye, like the lens of an ordinary camera, are subject to two optical defects—chromatic aberration and spherical aberration. White light is a composite of various coloured lights, which are isolated by the refractive media, and each undergoes a different amount of refraction (chromatic aberration); thus a blue light is focussed in front of a red light. The distance between the two is, however, extremely slight and passes unnoticed; there is no arrangement for correcting it. If, however, a red light and a blue light be fixed at equal distances from the eye, the red light, which requires the greater accommodation, appears to be the nearer of the two.

Rays of light entering close to the central axis of the refractive media are less refracted than those near the periphery. This is termed spherical aberration, and is corrected to some extent by the iris which acts as a diaphragm for cutting off the peripheral rays. In many eyes other defects are present but these arise from faulty constructions of the eyeball: thus if the eyeball is too short, hypermetropia or long-sightedness is present, if too long, a condition of myopia or short-sightedness results. With advancing age the ligaments of the

lens lose their elasticity, and accommodation therefore is more limited—a condition termed presbyopia. In a large proportion of cases the vertical and transverse curvatures of the cornea are dissimilar, hence horizontal and vertical lines in the same plane cannot be focussed simultaneously. This defect is called astigmatism.

Movements of the Iris.—The iris serves the ordinary functions of a diaphragm for the refractive media. It is controlled by two muscles, the sphincter (circular) which diminishes the size of the pupil, and the dilatator (radiating) which increases it. Its movements are purely reflex, i.e. quite involuntary; the afferent impulse passes back along the optic nerve to centres in the brain and spinal cord while the efferent impulses travel out by the nerves supplying the muscles of the iris.

FIG. 87.—Diagram to show the extent of the visual field of the right eye.



The circle indicates the ora serrata, and the shaded area of irregular outline represents the amount of the posterior part of the retina acted on by, and responding to, light when the eye is kept in one fixed position.

The two main factors that influence the size of the pupil are light and accommodation. When the eye approaches a bright light the pupil contracts; in a dim light it dilates. If the eye be accommodated for a near object there is always an accompanying contraction of the pupil; similarly when accommodation is relaxed the pupil dilates.

Functions of the Retina.—The light waves emanating from an object and focussed on the retina form the stimulus that evokes a visual sensation. The pathway by which the sensory impulses reach the cerebral cortex has already been described (p. 77).

All the nervous part of the retina, i.e. the portion behind the ora serrata, is sensitive to light, but for the distinct viewing of objects merely a small area of it, viz. the yellow spot, and more particularly the fovea centralis, is utilised. If the eye could be kept at rest and projected forwards from its bony cavity the outline of the visual field would be a circle corresponding to the ora serrata. From the situation of the eyeball, however, a certain amount of light is cut off by the overhanging eyebrows, by the nose, etc., so that the visual field is an area of very irregular outline varying in different individuals (Fig. 87). Although light as distinguished from darkness, is thus recognisable by a large area of the retina, yet only the images formed on the fovea centralis are seen distinctly; the farther from this region the image falls, the less distinct does it become. The elements of the retina that respond to light are the rod and cone bipolars. This can be

demonstrated in three ways: (1) the yellow spot, the region of most acute vision contains only rod and cone neurons; (2) at the region where the optic nerve enters the retina there are only nerve fibres—all the other layers are absent; light falling on this area which is described as the blind spot of the retina (Fig. 88), gives no sensation; (3) the bloodvessels of the retina lie in front of the layer of rods and cones and it is possible, by special devices, to see them. If in a dark room a bright light held at one side of the head be focussed on the eyeball which is directed towards the opposite side the branching retinal bloodvessels become visible. The experiment is best carried out by moving the light with a continuous circular movement since the peripheral portion of the retina on which the image is falling is easily fatigued.

The exact physical change that takes place in the layer of rods and cones is unknown. According to the generally accepted view, the light waves effect chemical changes in the visual cells, and the new substances formed act as stimuli. The theory originated from the discovery of the presence in the rods

FIG. 88.—To show the presence of the blind spot of the retina.



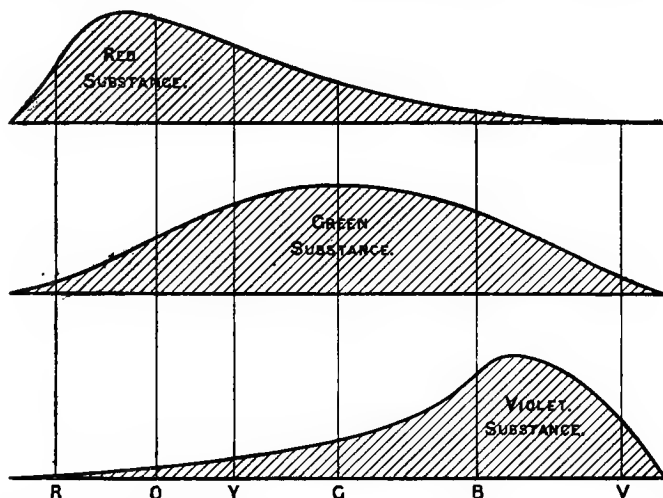
Close the left eye and gaze steadily at the cross with the right eye. Move the diagram to and from the eye. In one position the circle will apparently disappear.

of a purplish pigment—rhodopsin or visual purple—which is bleached by exposure to light. The layer of pigment cells that lies in apposition to the rods and cones acts as a medium for the regeneration of the visual purple. Since, however, visual purple is absent from the cones and therefore from the fovea centralis it obviously is not essential to vision.

The length of time during which a stimulus must act on the retina to produce a sensation of light is unknown, but must be extremely short, since flashes of light that are practically instantaneous are appreciated. Further the effect on the retina lasts longer than the stimulus, and this is more noticeable with weak than with strong stimuli. As a result of this persistence of effect, after-images can be recognised, and in addition if two or more stimuli follow in rapid succession their effects are compounded into a single sensation. The sensation of light is a complex sensation. Not only is the general form of an object realised but also its degree of brightness and its colours. The comparison of the relative brightness of two objects is mainly a comparison of the different strengths of the stimuli emitted by them; this, however, is obvious only when the two objects are of the same colour—a yellow light appearing as more intense than a red, etc. The amount of additional stimulus required to produce an appreciable effect follows Weber's law (p. 88); in this case the factor is about $\frac{1}{100}$.

Colour Vision.—The colours appreciated by the eye may be divided into two main groups : (1) those popularly designated colours, comprising the range of colours in the spectrum and the various combinations of these ; (2) the series of black, white, and the intermediate greys. The colours distinguishable in the solar spectrum are red, orange, yellow, green, blue, indigo, and violet ; when these are combined in proper quantities the sensation of white results. When an object neither reflects nor emits light it appears black ; this is a distinct sensation in itself and is not to be regarded as due to non-stimulation of the

FIG. 89.—Diagram to show the Young-Helmholtz theory. (Helmholtz.)



R, O, Y, G, B, V, indicate the colours of the spectrum. The vertical lines show the proportion of each substance required to produce one of the spectral colours.

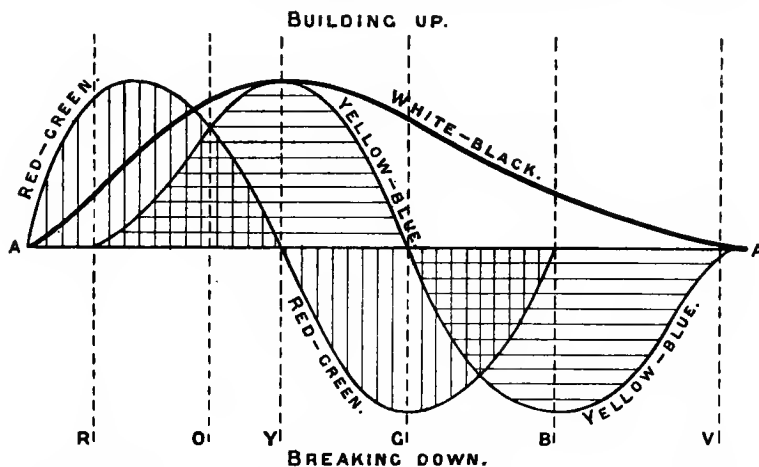
retina. Combinations of black with white form the greys ; white or black may be mixed also with any of the other spectral colours.

Colours may be combined on the retina either by exposing the eye to two or more colours simultaneously or by the use of rapidly revolving parti-coloured discs which permit colours to act in such rapid succession that their effects are fused. Although the solar white light is a combination of the seven colours of the spectrum, yet it has been found possible to isolate three colours, suitable admixtures of which will yield white or any of the other spectral colours. These three—red, green, and bluish-violet—are designated the primary or fundamental colours. Further, there are certain pairs of colours which on fusion produce white (grey) ; they are termed complementary colours. In a general way it may be stated that to every colour there is a complementary one ; those most commonly used in experimenting are : (a) red and greenish-blue, (b) orange and

blue, (c) greenish-yellow and violet. Two important phenomena are related to these facts: (1) if an observer gazes steadily for a few seconds at a bright light and then closes the eyes or looks at a white background, a coloured after-image is seen—in some cases the image is of the same colour as the original (positive after-image), in other cases it is of the complementary colour (negative after-image); (2) when two complementary colours are placed in apposition the colour of each becomes more vivid by contrast.

Some individuals are unable to differentiate all the colours of the spectrum—a condition known as colour-blindness; the commonest forms of this are red-

FIG. 90.—Diagram to show the Hering theory of colour vision. (After Foster.)



The spectral colours are indicated by R, O, Y, G, B, V. The vertical lines indicate the amount of each substance acted on to produce the respective colours.

blindness and green-blindness. In a typical case red, orange, and yellow appear as yellow, green as greyish-yellow or greyish-blue, indigo and violet as blue.

Theories of Colour Vision.—Three main theories have been advanced to explain the physical basis of the colour sensations. They are named after their authors: (A) Young-Helmholtz, (B) Hering, (C) Franklin.

(A) **THE YOUNG-HELMHOLTZ THEORY.**—Three primary colours, red, green, and violet are chosen and it is assumed that for each of these there is a special chemical substance present in the retina. The action of light is to break down these substances in varying proportions; black results when no chemical changes are going on (Fig. 89).

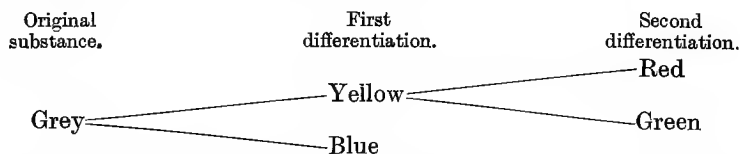
(B) **THE HERING THEORY.**—As in the preceding theory, the presence of three chemical substances is assumed, but from these, six sensations are derived;

from the breaking down of one of the substances a specific sensation results, another follows its reconstitution (Fig. 90). The substances are described as follows :—

Substance.	Effect of breaking down.	Effect of building up.
Red-green	Red	Green
Yellow-blue	Yellow	Blue
White-black	White	Black

(C) THE FRANKLIN THEORY.—According to this view, a chemical compound, described as the grey substance, exists in the rods and cones ; when light acts on it, white or grey sensations are evoked. In the periphery of the retina, this substance is present in its simplest form. In the cones, however, it is differentiated into components that react to colours. Thus in the greater part of the central zone of the retina, yellow and blue can act separately as stimuli ; together they give white or grey. In the fovea, and in a limited region around it, the yellow component is further divided and will respond to red and to green.

Schematically the theory may be thus represented :



This theory takes cognisance of the observation, that the rods and cones have different physiological functions (Fig. 91). The cones respond to white and black and to all the colours—the rods to only white and black. The cones are therefore adapted for use when the illumination is good ; in feeble illuminations the eye by means of the rods is able to recognise surrounding objects.

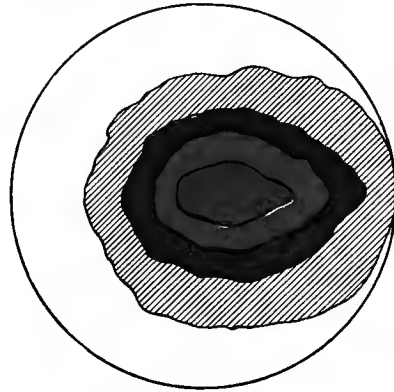
Binocular Vision.—So far, the main problems connected with vision, have been treated of, for a single eye. Normally, however, the two eyes are used for viewing objects, and special arrangements are therefore requisite to ensure that each object appears single. Each eyeball is capable of being moved in many directions by the ocular muscles. These act in balanced pairs ; thus the inner muscle of one eye usually acts with the outer of the other, etc., so that, under ordinary circumstances, the image of the object viewed falls on the fovea of each retina. Even when the eyes are fixed, however, objects still appear single, and this requires that in each retina there should be ‘corresponding points,’ stimulation of which gives rise to a single sensation. The inner half of one retina provides corresponding points to the outer half of the other and *vice versa*. This is one reason why the blind spot of the retina is not appre-

ciated, since the blind spot of one retina does not form the corresponding point to that of the other. Even when one eye is closed, however, the blind spot gives no sensation; it contains no receptive cells, and is totally neglected by the visual centres in the brain.

Visual Judgments.—In estimating the dimensions of an object, the size of its retinal image, which is inversely proportional to its distance, is an important factor; only when the objects are at the same distance is it the determining factor. For objects at varying distances, the judgment of their relative sizes depends practically on the appreciation of their distances, and is arrived at from the following data: (a) the size of familiar objects in their neighbourhood; (b) the atmospheric effects, haziness, blurring of outline, etc.; (c) muscular sensations arising from the amount of accommodation necessary to focus them, or, in binocular vision, from the amount of convergence of the visual axes.

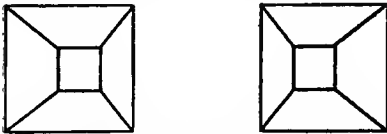
Solidity.—The image on the retina is a plane figure, but by the combination in rapid succession of the several aspects of an object, involving to-and-fro muscular movements, an estimation of its depth and form is arrived at. In binocular vision, the images on the two retinæ of a solid object are not exactly alike (Fig. 92). The right eye sees more of the right side of the object, the left more of the left. The fusion of these two dissimilar although closely related images, gives rise to the conception of solidity. The play of light and shade on the object is also an aid, and further, a previous knowledge gained through the pressure and muscle senses is associated in the judgment of form. Visual judgments are frequently at fault, as may be seen in Figs. 93, 94, and 95.

FIG. 91.—Diagram to show the extent of the field of vision for the primary colours. Right eye.



The central zone responds to all the primary colours; the second zone to blue, red and yellow; the third zone to blue and yellow; the outermost zone recognises merely light and shade.

FIG. 92.—Outlines of a truncated pyramid showing difference in the images seen by the two eyes.



If the reader relaxes his accommodation by gazing at a distant object and then interposes the diagram in the line of vision, still keeping the accommodation relaxed, the truncated pyramid will appear as a solid object.

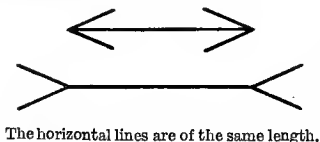
The Ear

Anatomically the ear is divided into three parts, external, middle, and internal. The receptive sensory cells are situated on the walls of the internal

ear, a structure of irregular form lying in the substance of the temporal bone—one of the bones of the side of the skull; the external ear and middle ear are accessory structures (Fig. 96).

External Ear.—The external ear comprises two portions: (1) an outer expanded part, the auricle or pinna which encircles an opening leading into (2) the external auditory meatus. The meatus is a short tube, about one inch long, open externally, but closed internally by a membranous partition called the tympanic membrane or drum of the ear. The tube presents a double convexity, upwards and backwards.

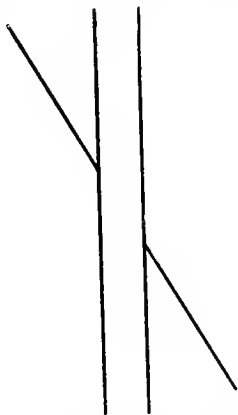
FIG. 93.—Müller-Lyer's figures.



The horizontal lines are of the same length.

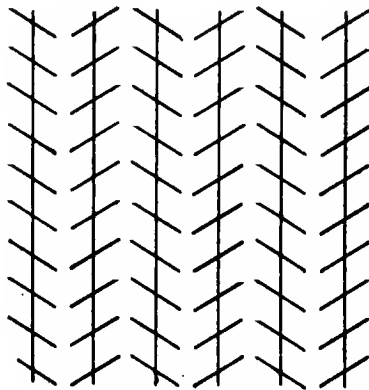
Middle Ear.—The middle ear or tympanum, is a slit-like cavity between the tympanic membrane and the internal ear. Opening into it in front is a canal, the Eustachian tube, which leads up from the throat immediately behind the nose, and through which air can enter the tympanum. By means of an

FIG. 94.—Poggendorff's illusion.



The two oblique lines are portions of the same straight line.

FIG. 95.—The parallel puzzle.

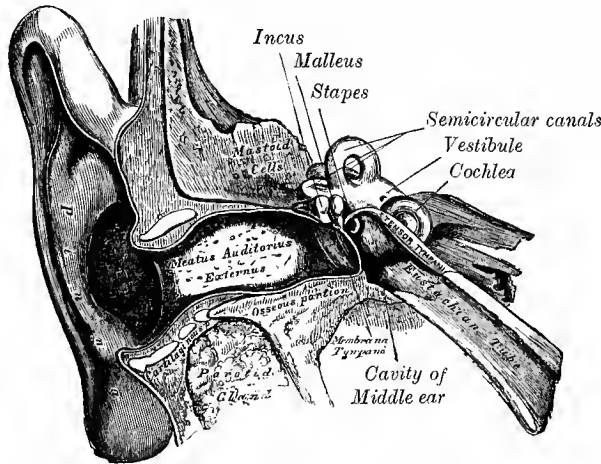


The vertical lines are parallel to one another.

opening above, the middle ear communicates with air cells in the substance of the temporal bone. In its interior are three small bones—the auditory ossicles—named the malleus (hammer), incus (anvil), and stapes (stirrup). The chief structure in the outer wall is the tympanic membrane which intervenes between the external auditory meatus and the tympanum; it lies very obliquely forming an angle of about 55° with the floor of the meatus. To the inner surface of the membrane is attached a process (the handle) of the malleus—the tip of the process reaching down to just below the centre of the membrane,

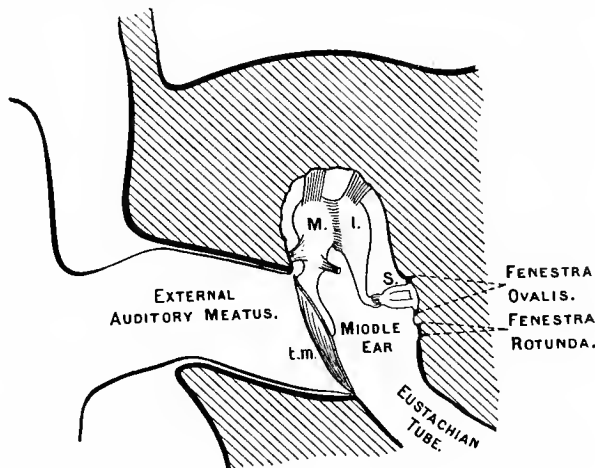
which is drawn inwards towards the tympanum. The membrane is thus somewhat funnel-shaped, and the apex of the funnel is known as the umbo.

FIG. 96.—A front view of the organ of hearing. Right side.



In the substance of the membrane are two sets of fibres : (1) fibres radiating outwards from the umbo to the periphery, (2) circular fibres grouped chiefly towards its circumference.

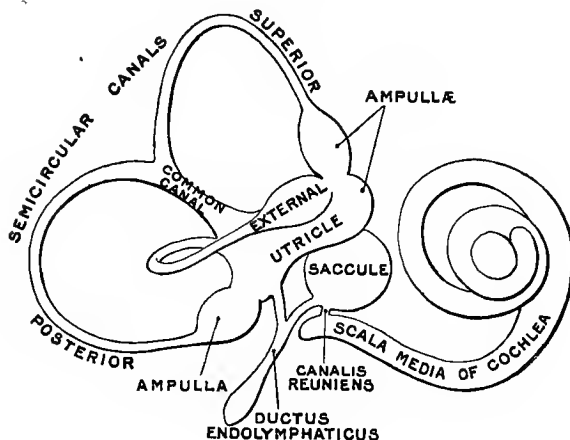
FIG. 97.—Schematic drawing of the middle ear to show the position of the bones within it; also the manner in which these bones are bound by ligaments to the walls of the cavity.



M. Malleus. I. Incus. S. Stapes. t.m. Tympanic membranes.

The greater part of the wall between the tympanum and the internal ear is bony, but in it are two small windows. The upper of these is the fenestra ovalis, and into it the

FIG. 98.—The membranous labyrinth. (Enlarged.)



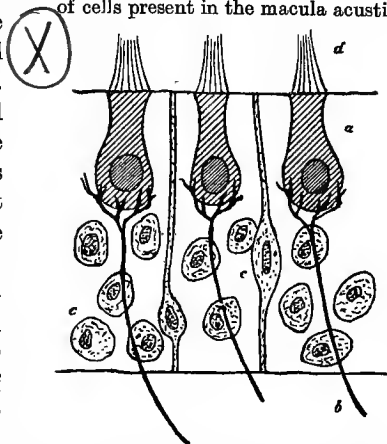
foot plate of the stapes is fitted; the other, the fenestra rotunda, is closed by a small membrane.

Of the three auditory ossicles (Fig. 97), the malleus is the outermost, the stapes innermost, and the incus is in the centre jointed to both. The handle of the malleus, as already mentioned, is attached to the inner surface of the tympanic membrane; into its upper

part is inserted a small muscle, the tensor tympani. The rounded head of the malleus articulates with the body of the incus; otherwise the bone is tied by ligaments to the tympanic walls. From the body of the incus a long process descends to articulate with the head of the stapes; like the malleus the incus is bound to the walls of the tympanum by ligaments. The stapes is stirrup-shaped; its head articulates with the incus, and just beside this a small muscle, the stapedius, is inserted; the base, which forms the foot plate of the stirrup, is fitted into the fenestra ovalis.

Internal Ear.—The internal ear consists essentially of a sac containing fluid—endolymph—suspended within another fluid—perilymph. In an early stage of development it is a simple sac, but later becomes so greatly modified that it is referred to as the membranous labyrinth (Fig. 98). It comprises two bulbs, the utricle and saccule, connected to one another by a Y-shaped duct—the ductus endolymphaticus. From the utricle open three semicircular canals,

FIG. 99.—Schematic view of the forms of cells present in the macula acustica.

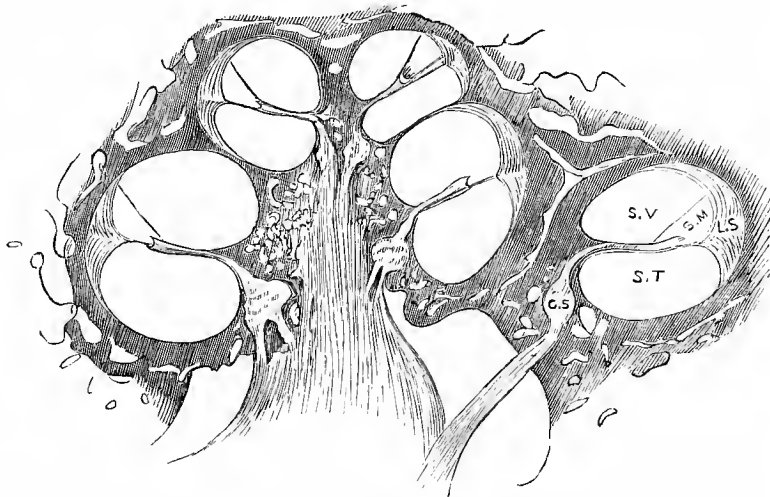


a, hair cells with *d* projecting hairs. b, dendrites of cells of vestibular nerve. c, supporting cells.

while the saccule communicates with a spiral tube, the cochlea. The bony cavities in which these are contained, form the bony labyrinth, and the subdivisions of this are practically those of the membranous labyrinth. Thus there are three bony semicircular canals and a bony cochlea, but the utricle and saccule lie in a common cavity termed the vestibule.

UTRICLE AND SACCULE.—On the anterior wall of each of these sacs is a thickening known as the macula acustica (Fig. 99). The thickenings consist of hair cells and supporting cells; the former are provided with long tapering

FIG. 100.—Longitudinal section of the cochlea, showing relations of the scalæ, etc.



S. V. Scala vestibuli. S. T. Scala tympani. S. M. Membranous cochlea. L. S. Spiral ligament.
G. S. Ganglion on cochlear nerve.

filaments that project into the endolymph within the sacs. Round the hair cells dendrites of the cells of the vestibular nerve are distributed. In contact with the hairs of the maculæ are rounded calcareous bodies called otoliths or otoconia.

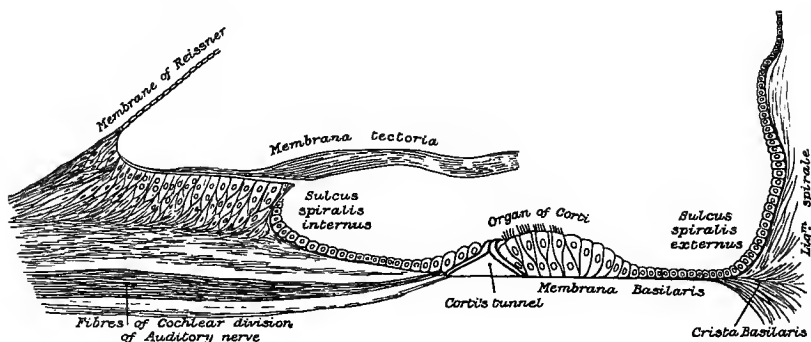
SEMICIRCULAR CANALS.—Three semicircular canals open into the utricle. Two of these (the superior and the posterior) lie in vertical planes at right angles to one another; the third (external) is horizontal and therefore at right angles to the other two. The vertical planes form approximately angles of 45° with the mesial antero-posterior plane; the canals of opposite sides are therefore arranged in parallel pairs. The two horizontal canals lie in planes parallel to one another; the posterior canal of one side is parallel to the superior of the other (Fig. 106).

One end of each semicircular canal presents a dilatation or ampulla. The non-ampullated ends of the posterior and superior canals are fused, and open

by a common opening, so that there are but five openings into the utricle. In each ampulla is a transverse thickening, the crista acustica, which, like the maculæ of the utricle and saccule, consists of hair cells and supporting cells. The dendrites of the vestibular neurons terminate round the hair cells.

MEMBRANOUS COCHLEA.—The membranous cochlea is a spirally coiled tube communicating with the saccule by a narrower portion, the canalis reuniens. The spiral tube is attached to the modiolus or central pillar and to the outer wall of the bony cochlea. Three channels are thus recognisable in the complete cochlea: (1) the membranous cochlea containing endolymph; (2) a channel above this, the scala vestibuli and (3) one below it, the scala tympani (Fig. 100). The two latter contain perilymph; they communicate with one another at the apex of the cochlea through a small opening termed the helicotrema,

FIG. 101.—Floor of membranous cochlea, showing the organ of Corti.



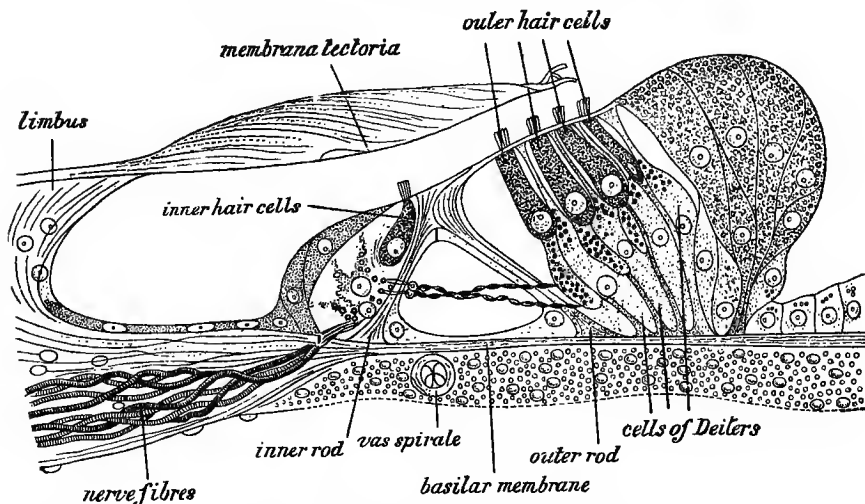
while behind they are continuous with the general perilymph space in which the utricle, saccule, and membranous semicircular canals are suspended. In the outer walls of the bony labyrinth are the two windows already described (p. 104); the fenestra ovalis opens into the vestibule, the fenestra rotunda into the scala tympani.

The membranous cochlea is triangular on cross-section. Winding round the modiolus is a spiral shelf of bone, the lamina spiralis, and to this the apex of the triangle is attached; the base is applied to the outer wall of the bony canal. The lower side of the membranous cochlea is attached to the margin of the spiral lamina and is known as the basilar membrane; the upper side is attached nearer the root of the lamina and is termed the membrane of Reissner. Both membranes extend across the bony cochlea, and are bound to the outer wall of this by a fibrous structure, the spiral ligament. The basilar membrane exhibits a series of transverse radiating fibres that increase in length from below upwards as the membrane increases in width. In the modiolus the ganglion of the cochlear nerve is situated, and from its cells

dendrites extend along the spiral lamina to a peculiar receptive structure on the basilar membrane—the organ of Corti.

ORGAN OF CORTI.—The organ of Corti is made up of hair cells supported by peculiarly-shaped rods. The rods are arranged in two serial rows, inner and outer, resting by broad footplates on the basilar membrane but inclining towards one another and finally jointed together at their other extremities. There are about 6000 inner rods and 4000 outer, and together they form the walls of a narrow channel, the tunnel of Corti (Fig. 101). Lying immediately exterior to the tunnel, on both sides, are hair cells and supporting

FIG. 102.—Section through the organ of Corti. (Retzius.)



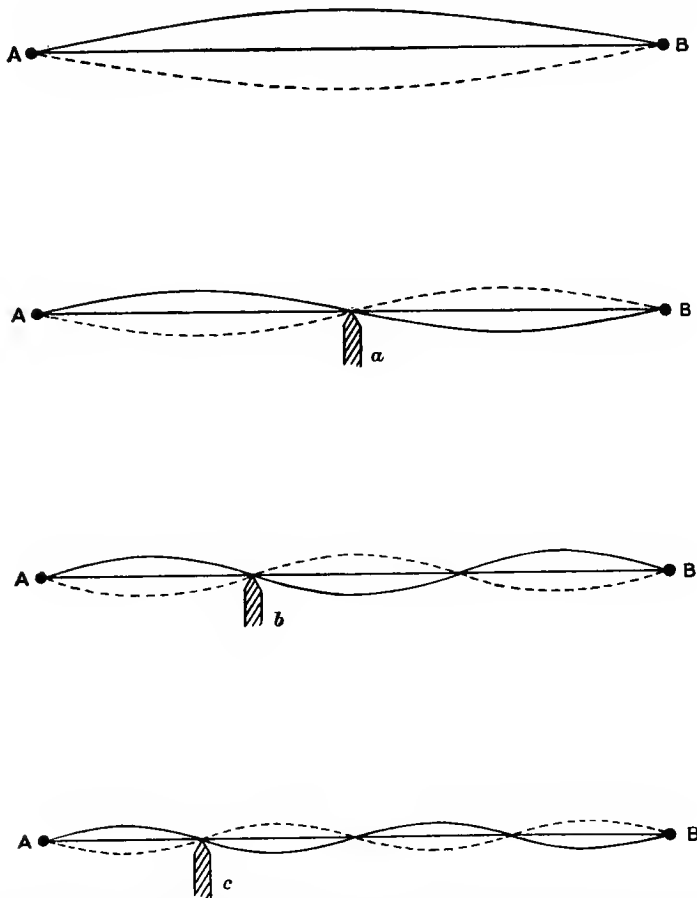
cells. At the free end of each of the hair cells is a small brush of about twenty hairs projecting through a fine reticular membrane (Kolliker's); round the other extremity of the hair cell, dendrites from the cochlear nerve end (Fig. 102). Roughly there are 12,000 outer hair cells and 3500 inner. Attached near the inner margin of Reissner's membrane and overlying the organ of Corti is a thick membranous structure termed the membrana tectoria.

Physiology of the Ear.—The internal ear comprises two functionally distinct organs. The cochlea is designed for the reception of sound waves, and impulses from it run inwards to the brain by the cochlear division of the auditory nerve (p. 79). The saccule, utricle, and semicircular canals transmit impulses which regulate the equilibrium of the body, and these travel to the brain by the vestibular division of the auditory nerve (p. 80).

The external and middle portions of the ear are accessory therefore to the cochlea.

Functions of the Cochlea.—The stimuli that originate the impulses in the cochlear nerves are the sound waves emitted by a sonorous body, but

FIG. 103.—To show the production of harmonic overtones in a vibrating string.



If the string, fixed only at its ends A and B, be plucked, the fundamental note is produced. If it be touched lightly at *a* the overtone of twice the vibration rate of the fundamental note (i.e. the octave) is produced. Similarly by touching at *b* or *c* notes with three or four times the vibration rate of the fundamental note result.

they are variously modified by the accessory structures before arriving at the hair cells on the organ of Corti.

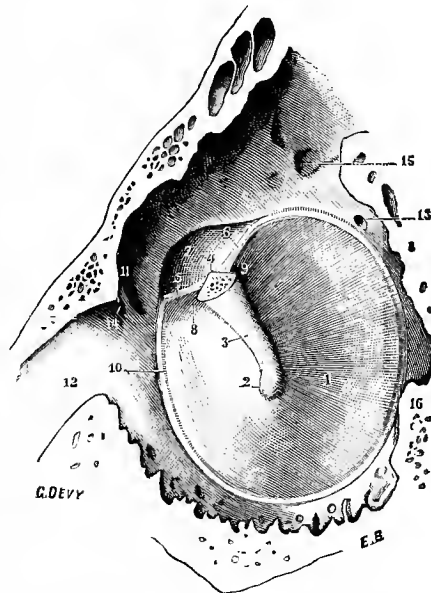
Sound waves consist of regular alternate compressions and rarefactions of the atmosphere (or other ponderable medium), and vary much in rate, in amplitude, and in form. A series of irregular compressions and rarefactions produces

a discord or noise. The three main characteristics of a musical sound are: (1) pitch, which depends on the rate of vibration—the slower the vibration the lower the note; (2) loudness, related to the amplitude of vibration; (3) quality or timbre, which varies with the form of the wave. Most musical instruments produce notes that are complex; each note has an outstanding component termed the fundamental note, but superadded to this are certain overtones. The rates of vibrations of the harmonic overtones are simple multiples (2, 3, 4, 5, etc.) of the vibration rate of the fundamental tone (Fig. 103). Most sound waves, therefore, are compound and as such reach the cochlea where they are resolved into their components.

In animals the pinna is capable of movements and of variations in form to enable it to collect the sound waves, but its function is practically in abeyance in man. The sound waves enter the external auditory meatus and set in vibration the tympanic membrane and the attached malleus. If the tympanic membrane were stretched equally in all directions, like the skin of an ordinary drum, it would vibrate only to its own fundamental tone. The attachment of the handle of the malleus is, however, eccentric, and thus the tympanic membrane is enabled to pick up and respond equally well to a great range of tones. By its connection with the membrane the malleus acts as a damper preventing the continuation of vibrations after the sound has ceased (Fig. 104).

From the tympanic membrane, vibrations are transmitted through the chain of ossicles to the base of the stapes, and set up waves in the perilymph of the internal ear. Although the ossicles are moveable, one on the other, yet for practical purposes they may be considered together as a bent lever, the fulcrum of which is determined by the attachments of the malleus and incus to the walls of the tympanum (Fig. 105). The distance of the tip of the handle of the malleus from the fulcrum is about one and a half times that of the base of the stapes from it. The stapes, therefore, moves through two-thirds of the

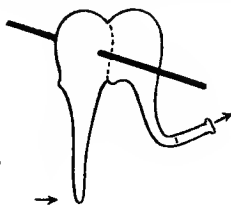
FIG. 104.—The tympanic membrane viewed from within. (Testut.)



1. Tympanic membrane. 2. Umbo. 3. Handle of malleus cut off from the rest of the bone. 12. Eustachian tube.

distance traversed by the umbo of the tympanic membrane, but at the same time with one and a half times the force. Two small muscles modify this mechanism: the tensor tympani can pull the umbo inwards and therefore tighten the membrane; the stapedius can press the base of the stapes into the fenestra ovalis and raise the tension of the perilymph. Pressure on the two sides of the tympanic membrane is equalised by free access of atmospheric air. On the outer side air enters by the external auditory meatus, while on the inner side air enters through the Eustachian tube, which is open during the movements of swallowing. The waves set up in the perilymph by the movements of the base of the stapes in the fenestra ovalis travel along the scala vestibuli, through the helicotrema, and down the scala tympani to the fenestra rotunda causing the membrane of this latter to vibrate. This membrane is a mechanical necessity whose only function is to allow the transmission of waves through the perilymph. The walls of the membranous cochlea are thrown into vibration

FIG. 105.—Scheme to show how the bones of the middle ear together constitute a bent lever with arms of unequal length.



by the waves passing through the perilymph; a wave motion is thus communicated to the endolymph. Finally these endolymph waves act on the hair cells of the organ of Corti and initiate the impulses in the cochlear nerves.

Under ordinary circumstances, therefore, the sound waves traverse first the atmospheric air, then the chain of ossicles, then the perilymph, and finally the endolymph. Sound, however, may reach the internal ear directly through the bones of the skull, as it does necessarily in cases where the tympanic membrane and ossicles have been destroyed by disease.

It is generally accepted that the movements of the endolymph stimulate the hairlets of the hair cells, and that an impulse is communicated by these to the surrounding dendrites of the cells of the cochlear ganglion. It is also generally believed that the cochlea is able to analyse sounds and therefore to modify the form of the endolymph wave. The manner in which this analysis is effected is still under investigation. It is a well-known fact in physics that an elastic string, such as a stretched piano wire, will pick out, and vibrate or resonate in sympathy with, atmospheric vibrations of its own period. According to the theory of Helmholtz, the basilar membrane provides a large resonating mechanism of this nature. He regarded the transverse fibres of the basilar membrane as so many elastic strings each with its own period of vibration. It has been pointed out that the fibres increase progressively in length from below upwards and therefore the low tones should be picked out by the fibres of the upper end of the membrane. When the basal part of the cochlea is destroyed experimentally in animals, they can (so far as one is able to judge) appreciate only low tones. If this theory be assumed, then, when a com-

pound tone agitates the perilymph, it is resolved into its components by the fibres of the basilar membrane. The hair cells connected with the affected fibres are stimulated—in a manner quite unknown—and the compound tone may or may not be reconstructed in the brain.

A theory advanced by Ewald regards the basilar membrane as vibrating in its whole length with a definite distinct wave motion for each tone; the hair cells on the summits of the waves are supposed to respond.

The telephone theory transfers the analysis of sounds to the cerebral cortex; the basilar membrane is compared to the plate of a telephone receiver which vibrates as a whole at different rates according to the periods of the sounds acting on it.

The human ear recognises as sounds, vibrations as slow as 30 per second or as rapid as 40,000 per second, but there is much individual variation. Two sounds following one another at intervals of more than 0·002 second can be perceived as separate sounds.

Auditory judgments, i.e. the appreciation of the position and distance of the sonorous body, are much less accurate than visual judgments. The apparent distance is usually determined from the intensity of the sound but both for this, and for the judgments of position, movements of the head are usually called into play, and in normal individuals the sense of vision is largely employed.

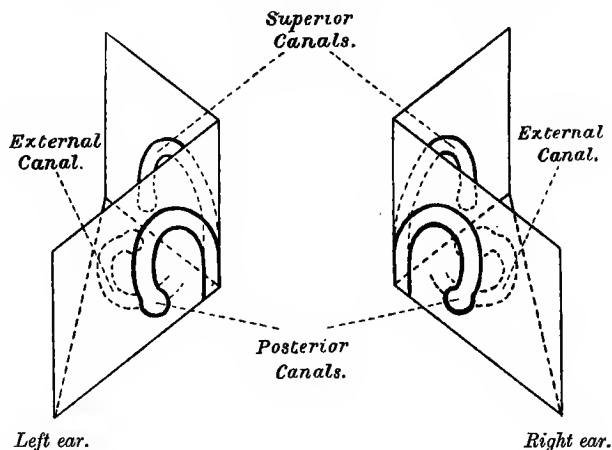
Functions of the Semicircular Canals.—The essential receptive parts of the semicircular canals are the hair cells in the ampullæ; round these the dendrites of neurons of the vestibular nerve terminate. As described (p. 80) there is no pathway for this nerve to the cortex of the cerebrum, consequently there is no consciousness of any sensation when the hair cells are stimulated. Nevertheless impressions are received by the canals, and the impulses resulting from them have an important effect on the equilibrium of the body.

The view that has obtained widest acceptance is that the stimulus arises from rotatory movements of the head setting up movements in the endolymph of the canals. If the head be moved in the plane of one of the canals the contained endolymph, by virtue of its inertia, lags behind, thus increasing the pressure at one end. If the end thus distended be the ampullated one the hair cells within it are stimulated and an impulse passes up to the brain.

The facts that provide the physical basis for this theory are: (1) the three canals lie in planes at right angles to one another and are thus adapted for interpreting movements in any of the three dimensions in space (Fig. 106); (2) the canals of opposite sides are arranged in pairs in such a manner that the ampullated extremities of each pair are stimulated by reverse movements, e.g. a horizontal movement of the head to the left stimulates the ampulla of the left horizontal canal—movement to the right, the ampulla of the right canal. Experiments on animals give considerable support to the theory. Two methods have been employed, viz. destruction of and stimulation of the individual

canals; it is probable that the ordinary methods of destruction of a canal produce stimulation of its ampulla. If, in a pigeon, the horizontal canal of one side be destroyed, the animal keeps turning its head from side to side and this movement is increased by the destruction of the horizontal canal of the opposite side. In a similar way, destruction of the vertical canals causes movements in a vertical plane; thus when the superior canal is destroyed, the pigeon turns head over heels, when the posterior are destroyed it turns somersaults backwards.

FIG. 106.—Scheme showing the arrangement of the semicircular canals in parallel pairs. The canals are viewed from behind.



The manner in which stimuli from these organs affect the muscles controlling equilibrium is still a subject of discussion; the most favoured theory is that each exerts an influence on the general tonus of a particular group of muscles.

Functions of the Utricle and Saccule.—So far, experiments have failed to prove definitely the physiological importance of these organs. That they are functionally closely associated with the semicircular canals rather than with the cochlea is indicated by the fact that their neurons form part of the vestibular nerve. It is thought that they may convey information regarding progressive movements as opposed to the rotatory movements recognised by the semicircular canals. The otoliths amongst their hair cells are supposed to exercise a dragging action on the hairs, and this, during movements, acts as a mechanical stimulus.

The Organ of Smell.

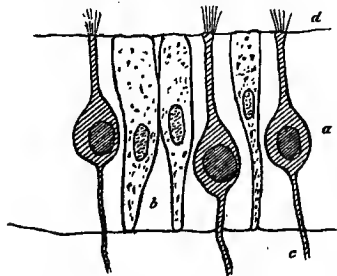
The receptive organ for the sense of smell is located within the nose, occupying on either side an area on the roof, outer wall, and mesial septum,

about 250 sq. mm. in extent (Fig. 107). In this area—termed the olfactory region—there are two kinds of cells : (a) olfactory cells, and (b) supporting cells.

The olfactory cells are modified bipolar nerve cells—one process, representing the dendrite, extends to the free surface where it terminates in a small knob, from which project six to eight fine hairs (Fig. 108); the other process, the axon, much longer, forms a filament of the olfactory nerve and runs up to the olfactory bulb where it ends in a glomerulus (p. 76).

Physiology of Smell.—The stimuli that excite the olfactory cells are certain chemical substances termed odoriferous. They must be presented in a gaseous or finely-divided form, and they reach the olfactory region in the inspired air or by diffusion. They are then dissolved in the fluid that bathes the olfactory cells, and act as chemical stimuli.

FIG. 108.—Schematic view of cells of olfactory region.



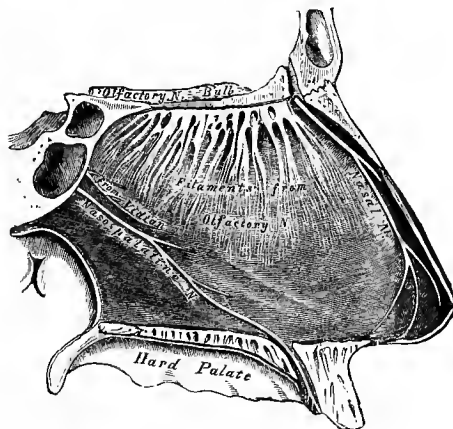
a. Hair cell with *d* projecting hairs. b. Supporting cells. c. Filament of olfactory nerve.

organ is, however, quickly fatigued for any particular odour, especially if it be a faint one ; this, however, does not affect its sensitiveness to other odours.

Several attempts have been made to classify odours, but all are unsatisfactory. The best is that of Zwaardemaker, viz. :

- I. Pure odours.
- II. Odours mixed with sensations of common sensibility.
- III. Odours mixed or confused with tastes

FIG. 107.—Nerves of septum of nose.
Right side.



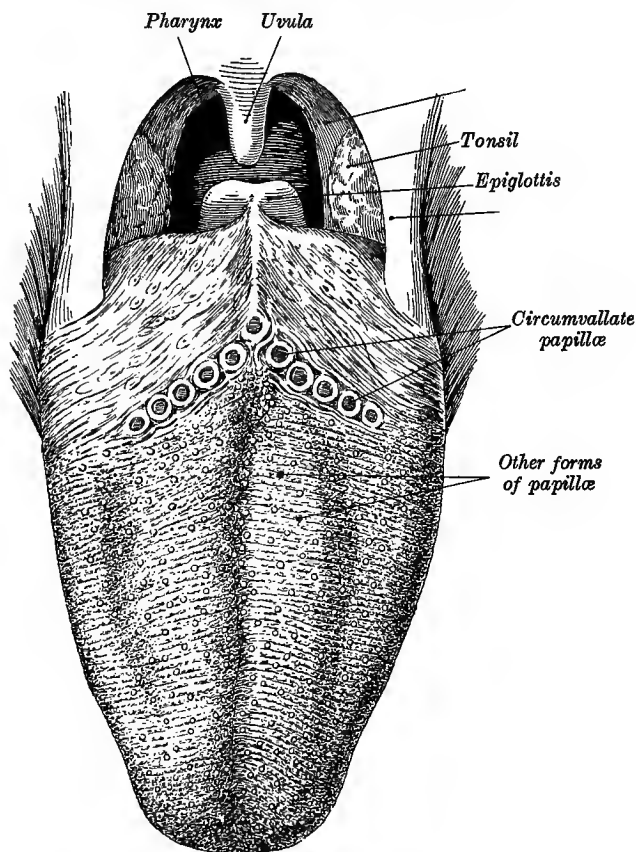
That liquids cannot act as olfactory stimuli unless they are volatile is shown by the fact that if the nasal cavities be filled with an odorous fluid such as rose-water, no smell is perceived. At the same time, unless there is sufficient moisture round the hair cells to dissolve the odorous substances, the sense of smell is greatly impaired, as is evidenced in cases of dryness of the lining membrane of the interior of the nose.

The sense of smell is very delicate in man but much more so in many animals. The human olfactory organ can, for example, recognise camphor in a dilution of $\frac{1}{400000}$, musk in a dilution of $\frac{1}{300000}$, etc. The

Pure odours are further divided into :—

- | | |
|-------------------------|---------------|
| 1. Ethereal. | 5. Garlic. |
| 2. Aromatic. | 6. Burning. |
| 3. Fragrant. | 7. Goat. |
| 4. Ambrosial. | 8. Repulsive. |
| 9. Nauseating or Fœtid. | |

FIG. 109.—The upper surface of the tongue.



When a mixture of odours is submitted to the olfactory organ the separate odours can generally be recognised. In some cases, however, the combination of odours gives no reaction ; thus if iodoform and Peruvian balsam be mixed in suitable quantities the mixture is odourless, or, alternatively, if iodoform be presented to one nostril and Peruvian balsam to the other no sensation of smell may be perceived.

The Organ of Taste.

The receptive cells for the sensation of taste are arranged in the form of taste-buds which are found chiefly on the tongue, but occur also in the soft palate and neighbourhood.

The taste-buds are distributed very irregularly over the tongue, but are most numerous on its upper surface. They are specially well marked along a Λ -shaped line near the back of the tongue (Fig. 109), where they are grouped on the sides of papillæ; these papillæ are designated circumvallate, from the fact that each is surrounded by a little trench and wall. Taste-buds are small ovoid bodies consisting of hair cells and supporting cells (Figs. 110 and 111). The hair cells form a group in the centre of each bud, the hairlets projecting towards the free surface through a small opening termed the gustatory pore; the supporting cells are arranged around them somewhat like the staves of a barrel. The terminal filaments of the nerves of taste surround the deeper ends of the hair cells. In the anterior two-thirds of the tongue the nerves of taste are the dendrites of cells of the geniculate ganglion—a sensory ganglion on the seventh cerebral nerve. The axons of these ganglion cells run inwards to the medulla and form arborisations around cells of a nucleus at the anterior end of the glosso-pharyngeal (ix) nucleus. The

FIG. 110.—Section of part of the papilla foliata—the papilla which contains the taste-buds on a rabbit's tongue.

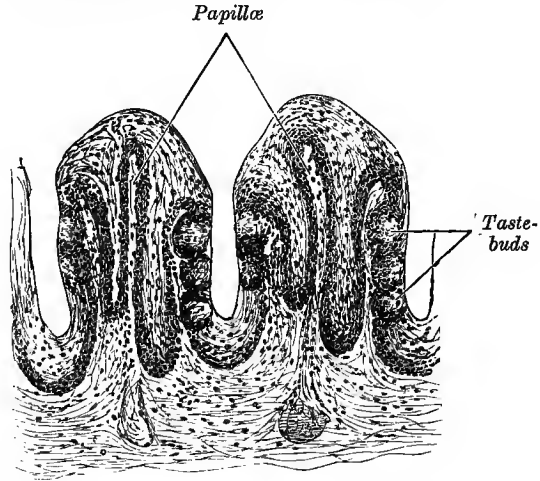
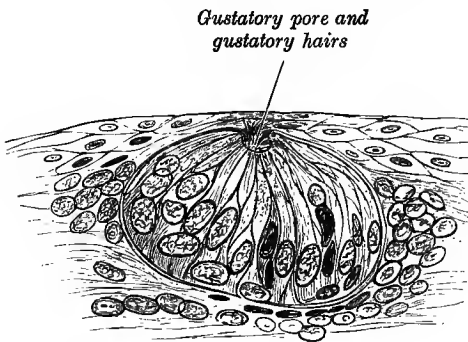


FIG. 111.—Taste-bud, highly magnified.



pathway is continued from this into the opposite mesial fillet and thence to the cerebral cortex. The nerves of taste for the posterior third of the tongue are dendrites of cells of a ganglion on the glosso-pharyngeal nerve.

The axons terminate round the glosso-pharyngeal nucleus whence the pathway of the impulses is continued through the opposite mesial fillet to the cerebral cortex.

Physiology of Taste.—The sense of taste is often confused with that of smell. If, for example, the olfactory region be destroyed or even temporarily interfered with, the taste of an apple can scarcely be distinguished from that of an onion. Again, a substance like pepper has no taste; the sensations caused by its introduction into the mouth are due partly to stimulation of the nerves of common sensation, partly to its odour. Before a substance can give a sensation of taste it must be in solution; the stimulus, like that of the sense of smell, is probably a chemical one acting on the hair cells of the taste-buds. Four primary or fundamental taste sensations are described, viz., sweet, bitter, sour or acid, salty. Different taste-buds may react differently to these substances, and as a general rule the taste-buds at the back of the tongue are the most sensitive to bitter, those at the tip and sides to sweet and acid tastes. The general view is that there are four different kinds of taste-buds for the reception of the four fundamental taste sensations. This is supported by the following experiments: (1) a substance such as sodium sulphate tastes salty if placed on the tip of the tongue, but bitter in the region of the circumvallate papillæ; (2) if the leaves of *gymnema sylvestre* (a tropical plant) be chewed, the sense of taste for sweet and bitter substances is temporarily lost, but acid and salty substances can still be tasted.

The delicacy of the sense of taste depends on the temperature of the solution employed, and is increased also by rubbing the substance against the tongue. The bitter and the acid taste organs are the most sensitive. When two or more substances are presented simultaneously to the taste-buds the effect of one may annul that of the others, but usually the individual sensations can be recognised.

Organs of General Sensation

Under the term 'general sensation' are included the sensations of pressure, temperature, and pain, and the muscle sense; all these were formerly grouped together as the sensation of touch. The word 'general,' used in this connection, refers to the fact that their receptive organs are widely distributed throughout the body. Anatomically a considerable number of receptive mechanisms connected with the neurons conveying the impulses that evoke general sensations have been described, but it has not been found possible to apportion these organs to the specific sensations. In many cases the receptive apparatus consists simply of an elaborate branching of the axis-cylinder of a sensory nerve; the medullary sheath is discarded and the ultimate fibrils ramify around cells of the skin or other tissues. A slight modification of this exists in the tactile cells of Merkel, where the ends of the fibrils form cup-

shaped expansions into which modified cells are fitted. In more highly specialised forms, the sensory fibres end in a semi-fluid substance, enclosed within a

FIG. 112.—End-bulb of Krause.

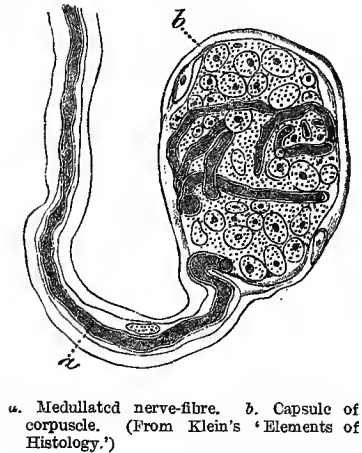
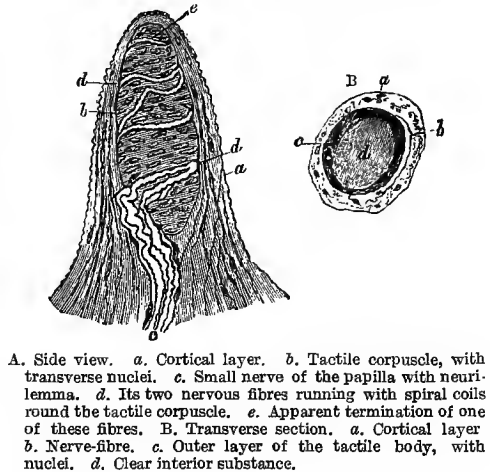
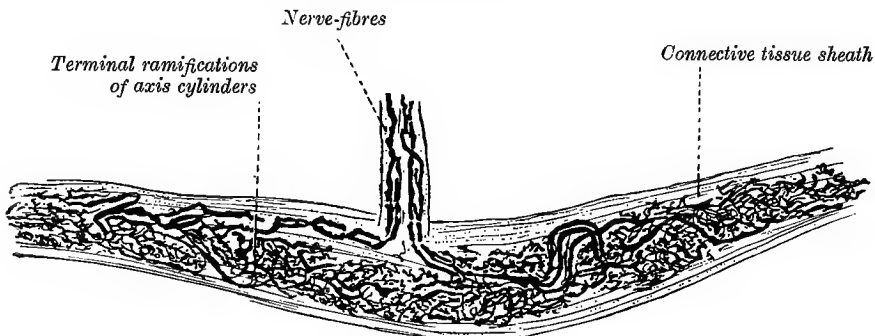


FIG. 113.—Tactile corpuscle of the hand.



fibrous capsule. Four special bulbous structures of this nature are described : (a) the end-bulbs of Krause (Fig. 112), (b) the genital corpuscles, (c) the

FIG. 114.—Nerve-ending of Ruffini.
(After A. Ruffini, 'Arch. ital. de Biol.,' Turin, t. xxi. 1894.)

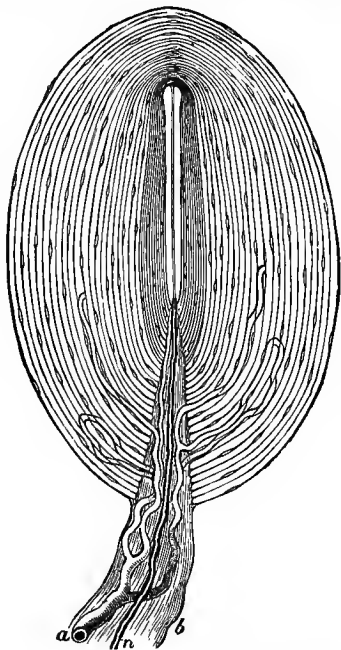


corpuscles of Meissner (Fig. 113), and (d) the corpuscles of Ruffini (Fig. 114). One (or occasionally more than one) nerve fibre enters the bulb, loses its sheath, and winds in an intricate spiral, giving off fibrils which form a close interlacement. In yet another type of receptive organ the capsule is thick and laminated like the layers of an onion ; in the centre is a core of semi-fluid

material, and in this the slightly branched naked axis-cylinder is embedded. Belonging to this group are (a) the cylindrical end-bulbs of Krause, (b) the Pacinian corpuscles (Fig. 115), and (c) the Golgi-Mazzoni corpuscles.

Definitely related to the muscle sense are organs found in muscles and tendons—the neuro-muscular and neuro-tendinous spindles (Fig. 116). Each spindle is composed of a group of special muscle (or tendon) fibres enclosed within

FIG. 115.—Pacinian corpuscle, with its system of capsules and central cavity.



a. Small artery. b. Fibrous tissue sheath.
n. Entering nerve-fibre.

a capsule. Ramifying on the outside of the capsule are several sensory nerves, which pierce at intervals, lose their medullary sheaths, and are distributed to the contained muscle (or tendon) fibres.

Physiological Differentiation of the General Sensations.—The receptive organs for pressure, temperature, and pain are very largely located in the skin where they are intermingled with one another, although each is distinct in itself. The sensation aroused in any of them is recognised locally at the area stimulated, and at the same time may be projected to the object which evokes the stimulus. It has recently been shown that on the exterior of the body each of these sensations is served by two sets of ingoing fibres arranged in different planes. The superficial fibres convey impulses that mediate the more delicate sensations, viz. minute differences in temperature, slight pressures, and tactile discrimination of closely adjacent points. These finer sensibilities are termed epicritic. By the deeper fibres pass the impulses that mediate the grosser forms of the sensations, viz. pain, wide

differences of temperature, and tactile localisation; these are designated protopathic sensibilities. Apparently the protopathic system exists in all organs and tissues but the epicritic is peculiar to the skin. The physiology of the protopathic fibres has not yet been fully worked out, and the greater part of the following details relates to the epicritic system.

Pressure or Tactile Sense.—The pressure sense has a punctiform distribution over the skin. The pressure nerves are distributed chiefly around the hairs, or where these are absent, to the corpuscles of Meissner and others. In different regions the skin varies in its sensitiveness to pressure stimuli as tested by ascertaining the smallest stimulus that will evoke a sensation. The power

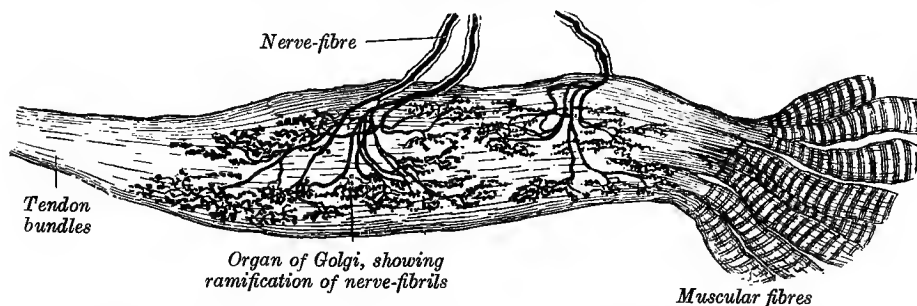
of tactile discrimination is not co-extensive with this local sensitiveness, but probably depends on the number of nerve terminations in a given area. Thus the skin of the face is more sensitive to a single stimulus than is the tip of a finger, but the reverse is the case as regards the ability to appreciate two distinct points.

The following are the results of some experiments to determine the approximate minimal distances that must separate two points before they can be recognised as distinct :

Tip of tongue	1 mm.
Tip of finger (front).	2 mm.
Middle of palm	8-9 mm.
Lip	9 mm.
Forehead	22 mm.
Back of hand	31 mm.
Back of neck	60-70 mm.

The power to recognise and discriminate with the pressure sense can be much improved by practice, as is obvious in the greater development of it in blind individuals.

FIG. 116.—Organ of Golgi (neuro-tendinous spindle) from the human tendo Achillis.
(After Ciaccio.)



Temperature Sense.—If the tip of a warm metal pencil be applied successively to different points on the skin, it will be found that while at some merely a sensation of touch is evoked, at others a distinct feeling of heat is experienced. Over the whole of the skin a series of heat spots of this nature can be determined. In a similar manner, by using a cold pencil, a series of cold spots may be marked out; these are not coincident with the heat spots and in fact are more numerous (Fig. 117). It is interesting to note that mechanical and electrical stimuli are capable of stimulating the cold spots. Further if a very hot (40° to 60° C.) pencil be applied to a cold spot the sensation of cold is aroused; a similar phenomenon is the feeling of cold on first entering a hot bath. The exact interpretation of it is doubtful, but it seems

probably due to the stimulation of the protopathic temperature fibres, while the simpler reactions of the heat and cold spots are characteristic of the epicritic system.

The minimal stimulus required to evoke a sensation from a heat or a cold spot varies in the different regions ; the tip of the tongue is the most sensitive, the trunk least.

FIG. 117.—A portion of the skin of the thigh showing the distribution of the heat spots and cold spots. (Modified from Goldscheider.)



Heat spots are coloured red, cold spots black.

Pain Sense.—If any of the sensory nerves of general sensation be cut and their central ends stimulated a sensation of pain results. This would seem to indicate that pain is merely an exaggerated pressure or temperature sensation, but more extended observations show that there are special nerve fibres, normally conveying pain impulses. Thus in certain diseases, sensations of pain may be completely lost while those of pressure and temperature remain. Again on going carefully over the surface of the skin with the point of a needle, a series of points can be marked out which give only a sensation of pain. These points correspond to the free nerve endings already described (p. 116), and they require a tolerably strong stimulus before they react. In the cornea the only receptive organs demonstrable are free nerve endings and in this region pain is the only sensation that can be elicited.

If a very strong stimulus of any nature be applied to the skin, pain may be felt, and the law which apparently determines this is : any stimulus that threatens damage to a part evokes a sensation of pain. Normally, cutaneous pains are localised with much accuracy, but the pressure and temperature sensations usually assist in the localisation. Pain arising from affections or

injuries of the internal organs is not, however, well located. In these organs epicritic sensibility is wanting, and the pain is frequently referred to the surface of the body. It is supposed that each segment of the spinal cord supplies part of an internal organ and the skin overlying. When pain is referred from the internal organ it is felt in the skin area supplied by the same spinal segment.

Muscle Sense.—The neurons that carry the impulses of the muscle sense towards the cerebro-spinal axis receive their stimuli through the neuro-muscular and neuro-tendinous spindles. Normally, the muscle sensations are always combined with sensations from pressure end-organs in the skin and joints.

Two distinct forms of the muscle sense may be recognised :

1. Sensations resulting from active movements of the muscles. It is these that are more particularly related to the neuro-muscular and neuro-tendinous spindles ; they are called into play in judging the force and extent of the movements, and on them are based judgments of weight, resistance, effort, and force generally. In combination with the pressure sensations they provide a stereognostic sense by which the form and solidity of external objects are ascertained.

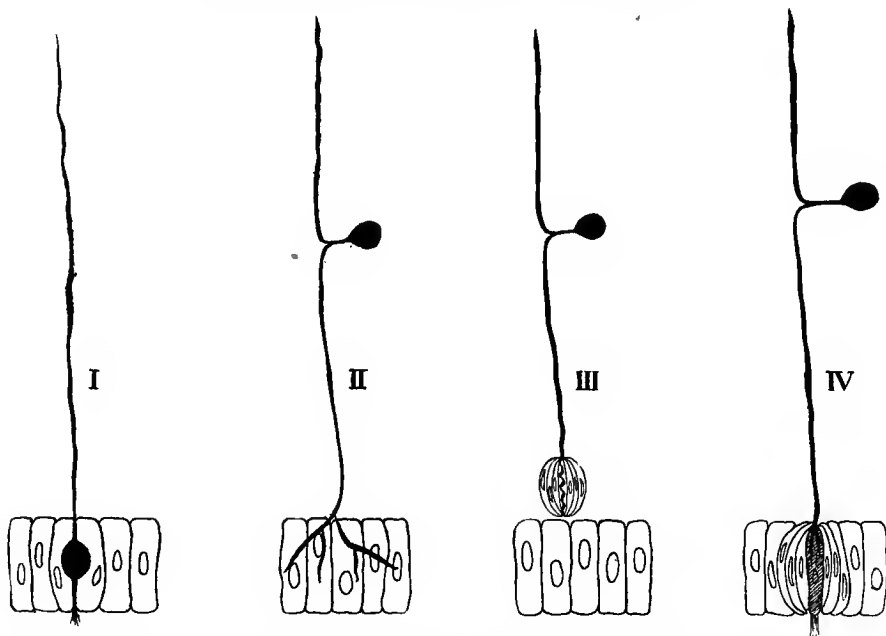
2. Sensations of position, evoked when either active or passive movements are carried out. Through these is gained a knowledge of the position of muscles and joints in relation to one another and to the rest of the body. Combined with the other general sensations they provide information regarding the position of the body, or part of the body, in space.

Many of the afferent impulses arising from the muscle spindles are not translated into consciousness, and there is a notable difference in this respect between individuals trained to observe sensations and those untrained. Whether a sensation be aroused or not, however, the ingoing impulses exercise an important influence over the voluntary muscles, and are apparently essential to the co-ordinated action of these, for any particular movement. The sensory neurons for the muscle sense take part in three distinct series of reflex pathways. In one the reflex centre is in the spinal cord ; in a second in the cerebellum, and in the third in the sensory-motor cortex around the fissure of Rolando.

Nerve Pathways for the General Sensations.—The fibres carrying impulses from the organs of the general senses are dendrites of cells of the spinal ganglia and of ganglia of certain cerebral nerves. The axons of these cells enter the cerebro-spinal axis and pursue different pathways, but most of the impulses conveyed by them ultimately reach the cerebral cortex behind the fissure of Rolando. The fibres conveying the muscle sense impulses make up practically the whole of the columns of Goll and Burdach. The impulses from the sense organs of pressure, temperature, and pain have each their individual pathways, and in addition there is for each a dual route—one route conveying epicritic, the other protopathic, sensibility. The epicritic fibres travel upwards in the columns of Goll and Burdach ; the protopathic fibres pass up in the antero-lateral basis bundle and cross to the opposite side of the cord before reaching the medulla.

The temperature and the pain fibres, shortly after entering the spinal cord, pass into the grey matter of the posterior horn. New relays of fibres carry the impulses upwards to the brain in the antero-lateral basis bundles and in the posterior longitudinal fasciculi. The temperature impulses reach the cerebral cortex, but the terminus of the pain impulses is quite unknown.

FIG. 118.—Diagrams to show types of sensory end-organs.



I. Olfactory organ. II. Pain organ. III. Pressure, temperature, and muscle sense organs. IV. Taste, hearing, and static sense organs.

Interior Sensations

There is a group of sensations, viz. hunger, thirst, warmth, cold, etc., which are always referred to the body itself. Their physiology is still very indefinite and no specific sense organs can as yet be described for them.

General Comparison of the Structure of Sense Organs

In Chapter I. it was pointed out that in the course of nervous specialisation large numbers of the cell bodies of sensory neurons were withdrawn from the surface and gathered together into ganglia near the cerebro-spinal axis. A comparison of the different types of sensory end-organs provides examples of

various stages of this translation inwards. (1) The olfactory end-organ retains most nearly the primitive position ; the nerve cell lies actually in the surface layer and the dendrite is very short. (2) The visual end-organs—the rods and cones—differ only in the fact that the necessary refractive media separate them from the surface ; otherwise the dendrites are again very short. In all the other sense organs the nerve cell is withdrawn to a deep ganglion, leaving a long dendrite extending to the periphery. (3) The pain end-organ is a simple dendritic branching amongst ordinary cells. (4) The end-organs for the pressure and temperature senses are more complex, in that the dendritic terminations are surrounded by modified cells. (5) The dendrites of the muscle sense neurons end in specialised cells. (6) The dendritic terminations of the nerves of taste, of hearing, and of the static sense (semicircular canals) are situated around special receptive hair cells. It is obvious then that practically the same form of end-organ may be utilised for the reception of widely different stimuli.

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